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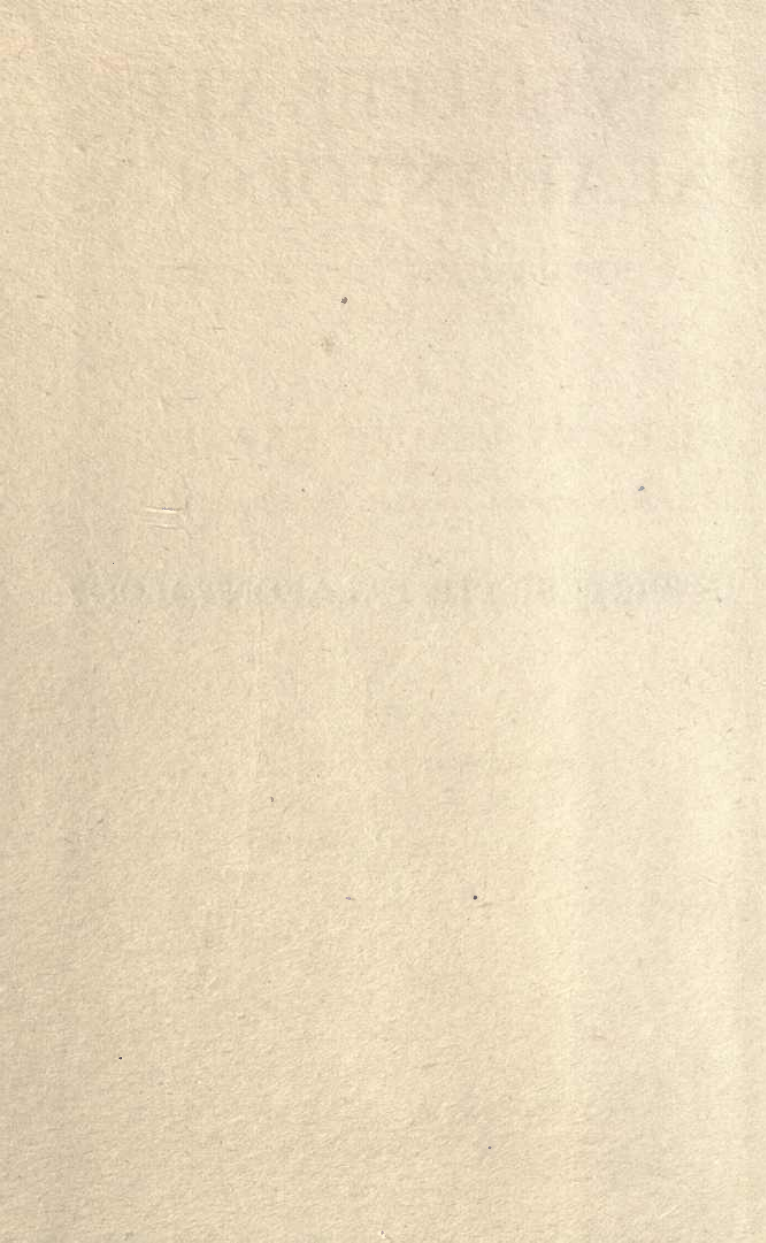
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INVERTEBRATE PALAEONTOLOGY



INVERTEBRATE PALAEONTOLOGY

AN INTRODUCTION TO THE STUDY
OF FOSSILS

BY

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WITH SIXTEEN ILLUSTRATIONS



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PREFACE

“THE following pages are dedicated to the service of those Admirers of Fossils who have not yet entered into a strict examination of the distinctive characters of these interesting substances.” Thus, almost a century ago, James Parkinson opened his *Outlines of Oryctology*. The “Study of Fossil Organic Remains” has advanced so far that the monographs of its pioneers retain little more than bibliographic and historical values. The apostolic succession of Palaeontologists is one of progress; while the great names of old are rightly held in reverence, the opinions and philosophies of early workers have no better claim to authority than the upstart “heresies” of the current generation. The truths that they discovered must endure for all time as imperishable foundations for the Science; their theories must be tried in the fire kindled by their research. If the test ends in destruction of old beliefs, let it be remembered that theory and hypothesis are the fuel without which the flame of Science would soon grow dim; and from the furnace flows an ever-growing stream of pure knowledge.

Nevertheless, the sentence quoted expresses the purpose and dedication of this book. Fossils are still objects of admiration (in both senses of the word),

whether their beauty captivates the eye or their complexity bewilders the mind. The brief chapters that follow are designed to encourage those whose interest has been awakened by the former sensation, and to smooth the path for those who require some palaeontological knowledge for furtherance of other studies. The various aspects of the Science are of necessity touched on but lightly. The ground-work of scientific inquiry is no more interesting, and almost less inspiring, than the learning of the alphabet. An average textbook must always bear to the Science of which it treats something of the relation of a Dictionary to Literature; it is indispensable, but lacks coherence and continuity. A monograph that thrills the soul of a specialist leaves others cold, if not indifferent. At the opposite extreme come the so-called "Popular" treatises on scientific topics. Too often accuracy is therein subordinated to simplicity—who could interpret Milton in words of one syllable?

An attempt has been made here to steer a middle course. The first part of the book, apart from sundry technical details, is intended to show something of what is meant by "Palaeontology." It is a common experience to encounter people who are horror-struck when told that an acquaintance is a Palaeontologist. When it is explained that he "goes in for" fossils, they are satisfied—the word is familiar, and they assume that they "know all about" the subject. But translation of Greek into Latin adds nothing to understanding of the matter concerned. Palaeontology can be called Oryctology, the study of Fossils, or "Antediluvian Biology," but the Science remains the same. It is hoped that the first section of the book may serve to

enlighten, though with a faint gleam, those who desire some explanation of the enthusiasm with which Palaeontologists pursue their research.

The second part is designed to give an epitome of the sequence of evolution as it has been unfolded in geological time. In the small compass of this Introduction to the Science there has been no space for the biological diagnoses that are necessary to make such an account intelligible. In consequence, it has seemed advisable to follow, in the main, the classification adopted in the latest and most comprehensive textbook of Palaeontology available in the English language. Except in the case of Echinodermata (which are discussed on the basis supplied in vol. iii. of Lankester's *Treatise on Zoology*), the various phyla are arranged in accord with the scheme given in the second edition of Zittel-Eastman's *Textbook of Palaeontology*, vol. i. The section is, in effect, a kind of condensed guide to that remarkable work. Although the present author has had occasion rigorously to suppress his own opinions in thus conforming to the views of others, the sacrifice involved seems worth while. In a multitude of counsellors there may be safety, but there is sure to be confusion. For a beginner, any *one* scheme is better than *two*.

A *via media* is often recommended as a safe course, but in truth such a path is full of pitfalls and beset with thorns. Scylla and Charybdis, and the more familiar dangers of the Devil and the Deep Sea, make the attempt of such a passage almost foolhardy. To such fellow-workers as may complain that their favourite aspects of the Science are ignored or slighted, I will apologize when they have succeeded where I have

failed. To beginners who find the book too abstruse or too dull I apologize herewith; and hope that some grain of interest or instruction may have survived their flails.

The illustrations, both photographs and drawings, have been made by myself. All of the former, and a large majority of the latter, are wholly new—they represent specimens in the collections of this Department. In the few cases where figures have been adapted from drawings previously published, acknowledgment is made; and, since such “copies” usually show some modification (apart from unintentional clumsiness of draftsmanship) from their originals, responsibility for their accuracy must fall on me.

To Mr. D. M. S. Watson I desire to express my extreme indebtedness for helpful criticism of the manuscript, and to Drs. F. A. Bather and H. Woodward my appreciation of their kindly interest and encouragement in this work, as in all that I have done. To these friends much of what is good in the book must be ascribed, whether directly or indirectly; for its many shortcomings they can in no way be held responsible.

H. L. H.

UNIVERSITY COLLEGE, READING,

January 1920

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UPPER PALAEOZOIC FOSSILS

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4. *Bellerophon* sp. Carboniferous Limestone, Kendal, Westmorland.
5. *Cyrtoceras nodosum*. Middle Devonian, Gerolstein.
6. *Glyphioceras crenistria*. Carboniferous Limestone, Poyll Vaish, Isle of Man.
7. *Phillipsia eichwaldi mucronata*. Carboniferous Limestone. (After Woodward.)
8. *Belinurus reginae*. Coal Measures. (After Woodward.)
9. *Slimonia acuminata*. Old Red Sandstone. (After Laurie.)

PLATE XIII

MESOZOIC FOSSILS

FIG.

1. *Isastraea explanata*. Corallian, Shellingford, Berks.
2. *Apiocrinus parkinsoni*. Bradford Clay, Bradford, Wilts.
3. *Paracidaris florigemma*. Corallian, Stanford in the Vale.
4. *Phymosoma koenigi*. Upper Chalk, near Kingsclere, Hants.
(The reconstruction of the apical system is hypothetical.)
5. *Nucleolites scutatus*. Corallian, Marcham, Berks.
6. *Micraster coranguinum*. Upper Chalk, Ecchinswell, Hants.
7. *Cyclothyris plicatilis*. Upper Chalk, near Newbury.
8. "*Terebratula*" *phillipsi*. Bathonian, Burton Bradstock, Dorset.
9. *Zeilleria digona*. Bradford Clay. Interior of dorsal valve.
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10. *Spiriferina* cf. *walcotti*. Lower Lias, Timsbury, Radstock.

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MESOZOIC FOSSILS

1. *Trigonia striata*. Bathonian, Burton Bradstock, Dorset.
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4. *Pleurotomaria reticulata*. Kimmeridge Clay, Weymouth.
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7. *Cosmoceras jason*. Oxford Clay, St. Ives.
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9. *Belemnitella mucronata*. Upper Chalk, Arreton, Isle of Wight.
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PLATE XV

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CAINOZOIC FOSSILS

FIG.

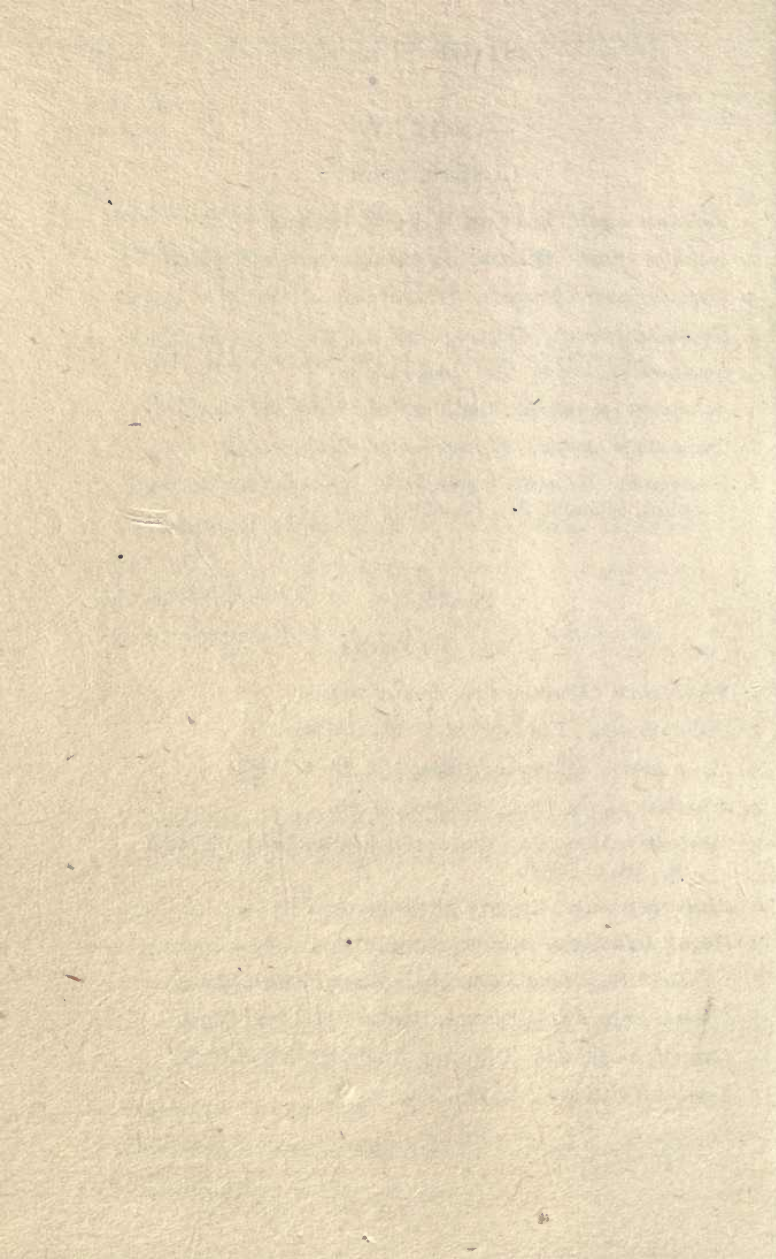
1. *Flabellum woodi*. Red Crag, Walton-on-the-Naze.
2. *Schizaster scillae*. Miocene. (Tubercular ornament omitted.)
3. *Clypeaster altus*. Miocene. (Plan of adapical surface.)
4. *Nucula headonensis*. Oligocene, Isle of Wight.
5. *Glycimeris glycimeris*. Red Crag, Suffolk.
6. *Aequipecten opercularis*. Coralline Crag, Sutton, Suffolk.
7. *Crassatellites sulcatus*. Eocene, Barton, Hants.
8. *Venericardia* ("Cardita") *planicosta*. Eocene (Bracklesham beds), Whitecliff Bay, Isle of Wight.

PLATE XVI

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CAINOZOIC FOSSILS

1. *Venus casina*. Coralline Crag, Sutton, Suffolk.
2. *Dosinia exoleta*. Red Crag, Walton-on-the-Naze.
3. *Nerita aperta*. Oligocene, Headon Hill, Isle of Wight.
4. *Ampullina patula*. Eocene, Barton, Hants.
5. *Turritella imbricata*. Eocene (Bracklesham beds), Whitecliff Bay, Isle of Wight.
6. *Batillaria serrata*. Eocene (Calcaire grossier).
7. *Volutilithes athletus*. Eocene, Barton, Hants.
8. *Surcula* ("Pleurotoma") *teretrium*. Eocene, Barton, Hants.
9. *Linnaea longiscata*. Oligocene, Headon Hill, Isle of Wight.
10. *Planorbis euomphalus*. Oligocene, Bembridge, Isle of Wight.
11. *Xanthopsis bispinosa*. Eocene, Sheppey.



INVERTEBRATE PALAEONTOLOGY

PART I.—MATERIALS, METHODS AND PRINCIPLES

CHAPTER I

THE SCIENCE OF PALAEONTOLOGY

(I) SCOPE

THE science of Palaeontology is concerned with organisms that have existed during periods of the Earth's history prior to the stage usually called "the present day." It is clear that there is no rigid line whereby Palaeontology can be separated from Biology; to-day will be "the past" to-morrow. The two sciences are intimately related and largely interdependent, just as Geology is linked with Geography. But Palaeontology cannot be treated as a mere branch of Biology; not only does the nature of its materials lead to adoption of widely different methods, but many of its problems are foreign to those confronting students of forms now living. If any logical connexion between the two sciences is to be maintained, Biology must be subordinated as a particular section, almost an aftermath, of Palaeontology. Such degradation would not meet with approval by Biologists, nor would it adequately express the relation between the two lines of inquiry; so that both must retain their independence.

Again, Palaeontology is very closely connected with Geology, especially with that section known as Stratigraphy. The traces of past life are embedded in stratified rocks, and cannot be interpreted successfully unless their historical sequence is proved. But it would be as reasonable to regard Biology as a branch of Geography (because distribution of existing life is an important factor in its comprehension) as to consider Palaeontology a section of geological science. Indeed, the study of Stratigraphy, though ultimately depending on the "law of the order of superposition," is practically impossible without the aid of fossil evidence; in many ways it is a kind of applied Palaeontology.

Hence the phrase with which this chapter opened is apt; Palaeontology is a distinct Science, with materials, methods and aims peculiar to it. It is largely dependent on, and no less contributory to, the sister Sciences of Biology and Geology. These branches of Natural History have been explored more fully, partly because of the longer application of study to them, and partly since Palaeontology could hardly progress until their principles were fairly established. But Cinderella has now reached the stage of adolescence, if not of maturity, and must take her place among the other members of the family. To press the simile too far would be unjust to the elder sisters—they are far from unlovely, and in no way senescent;—but it may be claimed that in Palaeontology there is to be found the peculiar fascination that surrounds the awakening possibilities of youth.

The scope of Palaeontology is wide, and has no definite limits. Theoretically its opportunities would commence with the first appearance of life on the Earth. Although recent research has revealed traces of organisms in rock-systems far older than many long regarded as "Azoic," it has thereby rendered painfully evident

the relative modernity of such evidence. On both geological and biological grounds, it is possible to argue that the records of life may cover but half, or less than half, of the history of life itself. It is thus with all forms of historical inquiry; knowledge passes back into uncertainty, uncertainty into legend, and legend into mythology; while beyond is a region where inference, and finally imagination, are freed from the inconvenient control of facts or even of verifiable hypotheses. It is not the purpose of the present work to roam through, still less to cultivate, those Elysian fields; so that the ultimate limit of palaeontological investigation may be taken at the oldest known fossil whose organic qualities are biologically demonstrable.

The opposite boundary of the province of Palaeontology is even less definite. At what distance from the feet of a Palaeontologist do the domains of Biology (in which territory he is a lifelong prisoner) come to an end? The carcass of the last member of a race now extinct would not serve as a landmark. It is at least possible that some species or variety that is in existence while these words are being written may have died out completely before they are read. The arrival of Man as an intelligent inhabitant of the Earth affords no better criterion, if only for the reason that the time of his appearance in that capacity is unknown. The Palaeontologist must needs study the fauna and flora of the current geological period, sharing with the Biologist the evidence thereby afforded, and applying it to the special problems with which he has to deal. In ordinary practice, the division between Biology and Palaeontology may be taken at the line where the Pleistocene is succeeded by the Holocene; but this is, at best, an ill-defined datum.

The indefinite character of its boundaries (a quality

shared with all other branches of Science) cannot obscure the main field of study that lies open to Palaeontology. Between the dim outlines of Pre-Cambrian faunas and the clearer, but bafflingly complex, details of present-day life, there extends a long range of fossil remains which supply certain, though fragmentary, evidence of the course of organic evolution. These fossils are the materials that form the basis of palaeontological science. Before proceeding to discussion of the varied conditions under which the evidence may occur, and the methods employed in its interpretation, it may be well to consider briefly the replies that a Palaeontologist could make to the questions so often asked of students of Natural Science: *Quo vadis?* and *Cui bono?*

(II) AIMS

Since Palaeontology is, in its essential aspects, Historical Biology, its aims must agree in large measure with those of Zoology and Botany. Many of the conditions and materials available to the latter Sciences are lacking in the evidence with which Palaeontology deals, so that in some ways its scope is curtailed; but the introduction of the historical element gives compensating extension in other directions. The fundamental and elementary aims may be summarized as the discovery, description and classification of organic beings, and subsequent deduction of the laws which have determined, and still govern, their life and relations. Palaeontology, the *discussion* of past organisms, must always be preceded by Palaeontography, their *description*. This is manifestly impossible until they have been discovered; so that the first and perpetual duty of a Palaeontologist is to collect fossils. The healthy, outdoor "sport" (for

such it may and should be) of "fossil-hunting" not only provides grateful relaxation from the relatively sedentary occupations of description and study, but enables the worker to pursue the latter with enhanced interest and understanding. No one can be qualified to discourse upon palaeontological topics who has not personally experienced the thrills and disappointments associated with work in the field.

When the three preliminaries have been attained, the aims peculiar to Palaeontology remain. The historical sequence in which living forms have arisen and disappeared is still a matter in which direct observation plays a dominant part, although it is of such a nature, and often so imperfectly displayed, that some opportunities arise for the exercise of argument. The distribution of forms of life at the present day (which still affords much scope for biological research) is no less important, though less apparent, when past periods are in review; many data of great geological importance can be determined by such phenomena.

Finally, when the succession of organisms has been sufficiently established, the ultimate philosophic aim of the science appears. The relations between the faunas and floras of the several periods, which can hardly be proved and yet may be confidently surmised, supply indications of the course, and to some degree of the process, of Evolution. Palaeontology, in this sense, may be defined as the science that deciphers the torn and blotted script in which the history of organic evolution has been written. Biology (using the term in a narrow and fortunately obsolescent sense) can suspect, and even experiment upon, the principle of evolution; but Palaeontology alone can trace the course of its progress, and display the broad views that are needed for appreciation of a process so slow and so far-reaching.

(III) USES

Palaeontology occupies an almost unique position among the sciences in that it has not, and can hardly be expected to acquire, an "economic" side. This quality of "purity" will prevent those who value science for its financial yield from devoting their energies to so "profitless" a study. To others, the absence of the taint of commercialism is not its least attractive feature. It is not that the science does not contribute, directly and indirectly, to human progress (such barren distinction pertains to sophistry, not to true philosophy); indeed, it may often possess that lowest of all attributes, a money value. The local "expert" who sinks a shaft for coal through graptolitic shales might save his own and his supporters' money by the use of elementary palaeontological knowledge. Nevertheless it must be confessed that discovery of a new fossil is not likely to produce the same kind of return that follows synthesis of a new dye, fabrication of a new machine, or even study of the life-history of insects or fungi. As a result, it is peculiarly easy for shallow critics to dismiss fossil-hunting as a futile hobby, suited to the requirements of a schoolboy who has tired of stamps and marbles, or to the ponderous dotage of a retired crank who has the means and leisure to dally with the few years remaining to him. Such critics would not be appeased by the reply that Palaeontology has a charm that inspires its devotees to perpetual and increasing service—they might justly argue that the same pleasant thralldom is exerted by gambling and other pursuits of doubtful profit and morality. But a Palaeontologist should not be an apologist for his science, when the vocations of prophet and evangelist are open to him.

Firstly, Palaeontology is a science, and would have

been classed, a few generations ago, as a branch of "Natural Philosophy." The desire to find out truth, in so far as it can be determined, is inherent in all human minds save those that have degenerated into the hopelessness of despair or the coma of satisfaction. All active brains are directed towards the endeavour to "see the wheels go round"; the same desire is there whether the wheels are those of a watch or of Fate. Acquisition of knowledge on any subject must add to the breadth of view of the successful seeker, and modify and extend his philosophy. Although it is true that a man may fashion his mode of life in defiance of his belief, it is self-evident that without some knowledge he could not formulate a substantial hypothesis whereby to steer his course. The quest for "knowledge for its own sake" appeals to some minds, but is difficult to justify outside the walls of a monastery. But when that knowledge is regarded as a contribution towards a better understanding of the forces and materials that surround and influence all living things, it appears not merely interesting or useful, but the one thing needful—a necessary precursor of the right and intelligent ordering of human existence. Viewed as a branch from the evergreen tree of Natural Philosophy, whose roots are Truth, Palaeontology seems no less fertile than its companion sciences. Its fruit may not be golden, but it has the compensating merit of being digestible and refreshing.

Secondly, Palaeontology is an indispensable ally of Stratigraphical Geology. Sedimentation, physiography and climate vary from place to place and from time to time, but the ordered sequence of organic evolution passes steadily forward. Local conditions may induce, or at least encourage, small modifications of structure in the organisms concerned, but the main current of racial life flows along its appointed course. Greater knowledge

of the trend of evolution, generally and in detail, leads automatically to improved precision in the interpretation of the records of Stratigraphy. It is sufficient to refer to the chaos of uncertainty that enshrouds the Pre-Cambrian era, and to compare that ignorance with the relatively clear understanding of such a period as the Jurassic, to show that Historical Geology is practically dependent upon fossil evidence. Of late years, detailed study of the palaeontological characters of Graptolites, Corals and Ammonites has revealed features of immense theoretical and practical importance to Stratigraphers. The long, and too often misleading, lists of fossils that occur in most stratigraphical papers are testimonies to the fundamental value of Palaeontology in such research. Not only do fossils supply evidence for comparative "dating" of rock-systems, but by the modifications and proportions shown by faunal groups, they indicate the conditions prevalent during their existence. Attempts to restore the physiography of past periods gain more reliable support from Palaeontology than from study of the lithology of sediments or even description of the known distribution of strata. It is not for a Palaeontologist to write an apology for the study of Geology, but he would be an unreasoning sceptic who doubted the practical value of that Science. And Stratigraphy, the culmination of Geological inquiry, depends almost wholly upon the evidence that Palaeontology alone can provide.

Thirdly, the archaic school of Biology that was content to restrict its activities to the study of existing organisms, regarding fossils as interesting, though sometimes inconvenient, "extras," is now well-nigh extinct. A student of human history who strove to understand and explain the intricacies of diplomacy that led up to the recent world war without reference to any events

prior to August 1914, would be in no worse plight than a Biologist who studied present faunas or floras without taking into account those that preceded and generated them. There yet remain biologists who dissipate their energies in efforts to fabricate schemes of evolution in defiance of palaeontological evidence; they have still to learn that the picturesque mists of hypothesis, however valuable where direct observation is lacking, must yield before the sunshine of truth as revealed by facts.

The conception of Evolution has been the guiding star of all recent biological study, however its interpretation may vary. It was not by accident that the two protagonists in the introduction of that doctrine, Lamarck and Darwin, were Palaeontologists of wide experience. Evolution might well have arisen as a theory among "pure" Biologists; but to Palaeontologists it is a manifest and proven principle. As to the determinants and expressions of this all-pervading law there is still ample scope for discussion and research. Recent palaeontological work has not only contributed much to the solution of these problems, but bids fair to supply more evidence to that end. The Biologist can suggest that certain methods of evolution might have been employed, and that certain courses may have been followed; it rests with the Palaeontologist to show whether or not such things have happened. When the extent to which belief in Evolution pervades all phases of human thought is realized, the value of the study of fossils is apparent. Indirectly, but none the less surely, it has enlarged the outlook of recent generations, while yet in its infancy as a Science. If such results have been achieved when the pioneering traverses are hardly completed, what may be expected from detailed survey of the territory comprised within the province of Palaeontology?

CHAPTER II

MATERIALS

(A) THE NATURE OF FOSSILS

(I) DEFINITION OF TERMS "FOSSIL" AND "PETRIFICATION"

THE name "fossil," which means "a thing dug up," was applied by early Geologists to objects that could be extracted from rocks, but that were not strictly samples of the rocks. It thus comprised separable minerals (particularly those in veins or geodes) as well as the curiously shaped "stones," of organic origin, as to whose characters much controversy existed. These two kinds of fossils were distinguished by the adjectives "native" and "extraneous" respectively, the latter types being clearly distinct from, and largely independent of, the rocks enclosing them. When continued study had plainly demonstrated the biological qualities of "extraneous" fossils, that non-committal adjective was replaced by the word "organized," and the expression "organic remains" became generally employed. At about the same time the term "petrification" came into frequent use, indicating that fossils had often become mineralized during entombment in the rocks. Gradually application of the word "fossil" to purely mineral specimens dropped out, and with its restriction to the "organized" kinds, need for qualifying adjectives disappeared. In its modern usage the word

“fossil” may be taken to refer to *those remains or traces of past life that occur in the rocks of the Earth’s crust, and afford biological evidence of their organic origin.* The last phrase in this definition excludes such phenomena as beds of graphite or masses of marble which retain no vestiges of organic structure, and give only presumptive evidence of organic origin.

The definition shows a certain lack of precision, for reasons similar to those that made limitation of the scope of Palaeontology impracticable. An empty shell lying on the beach, covered with sand by the wash of one wave, and laid bare by the scour of the next, has fulfilled the conditions required to assume the title of fossil; and the same qualifications would appertain to a body exhumed by order of the Home Secretary. If the shell were dug up from a prehistoric kitchen-midden, or the body disinterred from a tumulus, application of the term fossil would be only less inappropriate. Since organic structures may remain practically unchanged from very remote periods, it is useless to invoke the word “petrification” as indicating a criterion for the recognition of fossils. The ungainly phrase “sub-fossil” has sometimes been applied to those organic remains that occur on the border-line between past and present; but since the etymology of that term is grotesque, and its scope devoid of precision in both directions, its use rather aggravates the difficulty. In practice it is convenient to exclude organisms of the Holocene period from those that are called fossils, but such a division is purely arbitrary, and at times untenable. In some aspects of his work, a Palaeontologist is compelled to regard himself, and the living creatures that surround him, as potential fossils.

The introduction of the word “petrification” into the preceding paragraph demands a further definition.

Just as the name "fossil" has come to be used somewhat loosely (for example, as a mild term of abuse), so "petrification," both as a process and as a result, is often applied in cases where it is inappropriate. The two words are frequently treated as synonyms, but neither facts nor etymology support such identification. Passing over the obviously inaccurate use of the word in connexion with the products of a "petrifying spring" (where objects become coated with films of calcium carbonate precipitated from "hard" water), it may be stated that, while all petrifications are fossils, all fossils are not petrifications. The conversion into stone (or new mineral matter) that is implied by the latter term involves a considerable change in the substance petrified, whether it be achieved by Medusa's head or by less heroic methods. Petrification is believed to be carried out by molecular replacement, and will be discussed in a later section of this chapter; but a large proportion of fossils have undergone no such radical change. Impregnation of the spaces of originally porous shells with the same or some other mineral may possibly rank as petrification, since the process is similar to that whereby sand-grains become united into the "rocky" state of sandstone. But, in precise terminology, the word petrification must be restricted to *those fossils which have undergone change either by complete rearrangement of the molecules of the mineral of which they were composed* (when all minute structure is lost), *or by substitution of a different mineral* (when, if replacement has been gradual, details of structure may be retained).

(II) CONDITIONS NECESSARY FOR FOSSILIZATION

(a) *Biological*

Although in exceptional cases impressions, and even petrifications, of soft tissues have been found,¹ fossilization is not likely to follow the death of an animal that failed to secrete mineral, or other chemically stable, structures during life. Most purely organic tissues become dissipated by decomposition very soon after death, even if they escape digestion in the alimentary tract of a contemporary. Since a large proportion of Invertebrates now living, particularly of the simpler and smaller types, are without shells or skeletons, the existing fauna cannot be expected to leave an approximately complete representation for study by future palaeontologists. There is no reason to believe that the proportion of normally perishable forms was ever inferior to that at the present day—probably it was greater in more remote periods. Palaeontology is thus practically cut off from the study of a very considerable number of groups of animals; and, as a rule, can deal directly only with the hard parts of such classes as are capable of fossilization. Even among such structures, much diversity of durability exists. The hard parts of Invertebrates may be roughly classified as coherent or disjunct, and as siliceous, calcareous or chitinous. Coherent shells or skeletons (such as those of typical Gastropoda or Echinoidea) will retain their shape after dissolution of the associated soft tissues, and so may provide satisfactory evidence of the form and characters

¹ The frozen carcasses of animals preserved by "cold-storage" in Arctic regions since the Pleistocene period are, geologically considered, transient, and could not survive any climatic changes that raised the temperature of their surroundings.

of the animals that built them; but those that are made up of loose scales or ossicles (*e.g.* many Sponges, Holothurians and Arthropods), held in place by muscles or ligaments, will collapse into fragments on the death of their owners, and reconstruction will be a matter of difficulty and uncertainty.

The few animals that build skeletal structures of silica (chiefly Radiolaria and Sponges) secrete that mineral in the opaline or amorphous condition—its least durable form—liable to removal by solution in alkaline water. Calcareous shells or skeletons are sometimes made of calcite, a form of calcium carbonate which is relatively stable (see Pl. iii. fig. 4), but none the less readily soluble in acidulated water; those that are composed of the rhombic Aragonite are particularly prone to solution and decay (see Pl. iii. fig. 5). Chitin, which is an organic substance far more stable than ordinary soft tissues (comparable in this respect with the woody fibre of plants), can be preserved only if hermetically sealed up soon after death (see Pl. iv. fig. 1); even then it often passes into a carbonized and partly collapsed condition. Even when mixed with various salts of lime (as in many large Crustacea), it is still transient if exposed to atmospheric action. Hence the possession of shelly structures in no way ensures the fossilization of an organism, although it is necessary if such a consummation is to be normally attainable.

Again, secretion of mineral matter is the especial attribute of animals in adult stages; it is rarely or but feebly developed in young or larval forms. Hence a large proportion of the material available for palaeontological study consists of fully grown specimens; early developmental stages have rarely left recognizable traces. Since the history of an individual life seems to present an epitome of the evolution of the race to

which the organism belongs, it is logical to surmise that the earlier members of shell-bearing orders will have been relatively, or even absolutely, soft-bodied. As far as the evidence goes, this assumption seems correct. The early Molluscs and Brachiopods had very delicate shells containing much chitin, while many later members of those groups possess very massive calcareous coverings. It is at least possible that the perishable nature of early representatives of Invertebrate phyla may account for the lack of evidence of the evolution of great groups from one another. This question will be discussed more fully in Part II. Chapter I.

The habitat and normal mode of life of an animal strongly affect its chances of fossilization, apart from the influence they may have on the development of its skeletal structures. Early and effective burial of the remains is essential for preservation of the most massive mineral fabric; for rain-water, temperature-change and bacterial action disintegrate exposed shells even more rapidly than they destroy the rocks. Since it is more usual for detrital rock-matter to be removed from a land surface than for it to accumulate there (save for temporary stoppages in the transport system), the opportunities for rapid or permanent burial of terrestrial or fluviatile animals are rare. With few exceptions, Invertebrates that live in the air, on land, or in fresh-water, build far less solid hard-parts than those inhabiting the sea. This is partly due to the frequent lack of dissolved mineral-matter available for the former kinds, and partly because of the need for lightness and agility. Unless the remains of such animals become quickly drifted to a suitable burying-place after death, their permanent preservation must be very exceptional. The extreme scarcity of fossils in such terrestrial or inland-water deposits as the Old Red Sandstone, the Trias,

much of the Wealden and the Reading clays, need not be ascribed to a paucity of fauna; it is more probably due to the causes mentioned above.

The sea is the chief receptacle for the products of rock-wastage, and it is a fortunate coincidence that the majority of shell-bearing Invertebrates (excluding the Insects) are marine. Deposits accumulate in greatest bulk, and most rapidly, in the "detrital zone," which extends over the usually shallow parts of the sea around coast-lines. Again the satisfactory phenomenon can be recorded that the richest zones of Invertebrate marine life (perhaps excluding the Protozoa) coincide very nearly with the belt of coastal water where prompt burial is most likely to follow death. Further, rocks of the detrital zone are the most favourably situated for subsequent elevation, so that the fullest records of past life available for palaeontological study are normally those of the denizens of the marginal tracts of the sea. Organisms left upon, or drifted to, the beach will almost certainly suffer from the abrading influence of waves, and may become exposed to atmospheric weathering. The larger Invertebrates of deep water are, for the most part, inefficiently clad in mineral armour, and hence are not well adapted for preservation intact. The ideal situation for fossilization is in the shallow water below the level of low tides, where the scour of currents and waves is insufficient to prevent deposition of fine silt. Corals, Sea-Urchins, Brachiopods, Molluscs and Crustaceans are the groups that abound, or have flourished, most in such surroundings; their remains constitute the chief part of the palaeontological evidence available for study of the larger Invertebrates.

(b) *Geological.*

Possession of durable structures, and selection of a locality favourable for burial, in no sense ensure fossilization. The nature of the materials in which shells are embedded, and the geological influences that may operate on them, must inevitably affect the preservation of fossils. The three types of sedimentary matrix which most frequently contain fossils are those known as arenaceous (sandy or gritty), argillaceous (clayey), and calcareous (ooze or shell-sand). When such deposits are formed under marine conditions, it is usual for the first-named type to occur on or near the beach, for the second to accumulate in the outer part of the detrital zone, and for the third to be spread over the shallower parts of the open ocean. Some calcareous rocks, such as oolites and shell-limestones, are developed in the position normally occupied by sand. Although no definite line can be drawn between the three types of sediment, owing to the frequent intermingling of their ingredients, when relatively pure they afford very different matrices.

Sand is largely composed of worn grains of quartz, the hardest and most durable form of silica, and is likely to enclose abundant remains of shell-bearing Invertebrates owing to its littoral distribution. But it is eminently porous, and percolating water, which cannot attack quartz, will find in the calcareous shells material relatively easy to dissolve. Sand-burial thus affords but poor protection from the weather. The enclosed remains may occasionally become petrified by replacement, if the water that dissolves them holds some less soluble salts in solution; but more often they are entirely removed. If the arenaceous rock has been compacted before the dissolution of the shells, casts and

moulds will be left, representing the fossils in negative (see Pl. vi.). But if solution takes place before the sand has become consolidated, the grains close in to fill up the gaps, and no traces of fossils may remain. The soluble mineral matter is carried away by percolating water, to be redeposited elsewhere as a cement between the sand-grains or as a filling for cracks in neighbouring rock-masses. Further, the intense hardness of the quartz and other grains, when compared with that of calcite or aragonite, causes application of even gentle pressure to destroy the finer details of shells. The resulting pitted surface, often with difficulty disengaged from the penetrating sand, bears little or no resemblance to that of the original shell, even if the fossil has escaped comminution in its uncongenial surroundings.

Clay, being made of minute flakes of soft, micaceous material, and being practically impervious to water, has neither of the disadvantages of sand as a matrix for preservation of fossils. In such deposits as the Gault or the Barton Clay, fossils often retain their original "mother-of-pearl" sheen, and present all the details of their ornament as clearly as recent shells. Even chitinous or ligamentous tissues may be preserved almost unchanged. But in spite of these good points, argillaceous rocks are liable to develop two qualities that have a baneful influence on their contained organic remains. The flaky and waterlogged condition of the materials that give the "clay" character can persist only in uncompressed silt. Prolonged deposition brings the earlier formed parts under the weight-pressure of overlying sediment, with the result that the small flakes are rearranged in parallel layers, and included water is squeezed out. The shale thus formed shows great reduction in thickness from its previous bulk, and com-

pression is bound to involve all but the most massive of its "extraneous" contents. Hence fossils preserved in shales are normally flattened, the small quantity of clay that filled their cavities being reduced to an almost negligible film (see Pl. iv. fig. 4). Not only does this process result in loss of form, but it frequently causes the two sides of the fossil to be telescoped into one another, with very confusing effect. The difficulty of reconstruction of extinct types whose detailed structure cannot be deduced from study of living relatives is greatly increased when the characters of both surfaces are thus combined. Painful examples of this unfortunate type of preservation are afforded by the Sea-Urchins and Starfish found in argillaceous flagstones of the Lower Ludlow series. Secondly, the impermeable nature of a clay matrix, while effectively excluding destructive action from without, no less efficiently encourages chemical changes within the rock. Even the purely soft tissues of organisms may be buried in the silt, and by their slow decay give rise to various volatile substances, such as sulphuretted hydrogen, that strongly affect minerals doomed to association with them. The production of Marcasite (see Pl. v. fig. 2) (an unstable form of Iron sulphide) and Selenite (Sulphate of lime) are two frequent results of such reactions, and often these two wholly crystalline minerals afford the sole evidence of previous existence of fossils in clay. Nevertheless, in spite of these two serious disadvantages, clay is the best medium for the preservation of fossils.

A calcareous matrix is no less porous than an arenaceous one, but the similarity between its physical properties and those of the contained organic remains (supposing these to be made of calcite) mitigates the dangers to which the latter are subject. Although the

bulk of a calcareous rock is organic in origin, and thus in some measure crystalline, a large proportion is so finely comminuted that it reacts almost as if it were amorphous. Hence the "matrix" of a limestone usually proves more readily soluble in atmospheric water than the shells that it includes, and these are in consequence less likely to be seriously harmed (see Pl. i. fig. 2). (If the fossil is made of Aragonite, Opaline silica or Chitin, solution, decay or petrification is almost inevitable.) It is usual to find a secondary infilling of calcite, derived from percolating water, occupying all the smaller cavities in the shell-tissue, but this need not obscure the original structure. Again, the matrix consists of material which is theoretically of the same hardness as the enclosed fossils, and which in practice is softer owing to its powdered condition. Hence the pitting that so often defaces shells in sandstones is unlikely to be impressed on those in a limestone.

Except in mines and borings, fossils can be collected only from rocks exposed at the Earth's surface. Such rocks are always undergoing destruction by weathering agencies, and the fossils they contain must submit to the same fate, however "extraneous" their origin. Thus the most perfect and complete preservation is but temporary in relation to geological time. In many districts sedimentary rocks thousands of feet in thickness have been removed by denudation at various geological periods, and no vestiges of their faunas are preserved, save for occasional water-worn relics embedded in later deposits, or chance occurrences in the pebbles of conglomerates. But the tool of erosion is double-edged, and brings to light fossiliferous rocks that would otherwise remain buried and out of reach. Other and more merciless agents may work havoc on rocks and fossils, without affording a chance for rescue by collection.

Hypogene forces, which produce metasomatism in rock-masses buried to a great depth or involved in crustal movements, may cause distortion, recrystallization, or even magmatization of materials affected. An essential feature of such action is the re-grouping of molecules, either into new crystals of the original minerals, or into entirely fresh mineral types. A quartzite may occasionally retain rough indications of the fossils that were once embedded in it; the refractory nature of quartz tends to reduce its reaction to metamorphic forces. But a clay-slate, in which the annealed micaceous flakes have slewed round to positions different from those due to sedimentation, will involve its contained fossils in the distortion and cleavage to which it has been subjected. Phyllites and schists have undergone such complete recrystallization that neither the original rock nor its contents are clearly recognizable. Similarly, a marble results from complete rearrangement of the calcite molecules of a limestone; the saccharoidal complex of crystals retains no biological indication of organic origin. Finally, when heat and pressure are applied in full force, rock-matter undergoes that magmatic "fusion" or intersolution that results later in formation of "Igneous rocks." In these no suspicion of organic structure or influence, possibly excepting diamonds, can be expected to occur. The longer a rock has existed, the greater has been its danger from hypogene forces. Hence the record of the faunas of ancient periods of the Earth's history tends to become more imperfect as it becomes more remote. Extraordinary exceptions, such as those afforded by the wonderful Cambrian fossils of British Columbia, or the almost "Tertiary" quality of the Ordovician clays of Northern Russia, serve merely to emphasize the tragic deductions latent in this generalization.

(III) IMPERFECTION OF PALAEONTOLOGICAL EVIDENCE

The account of the conditions necessary for fossilization given in the preceding paragraphs shows clearly how rare must be fulfilment of those conditions. But the three essentials there indicated (which may be summarized as possession of hard-parts, a mode of death not involving destruction of the shell, and a place and medium of burial whence agents of decay are excluded) by no means include all that is required for fossils to become "palaeontological evidence." For such a consummation, the rock in which the organism has been entombed must remain on, or be elevated into, dry land; it must be exposed by natural or artificial excavations; and it must be visited by a "fossil-collector" at the precise time when the stratum has been laid bare. Even then there is always the possibility that the fossil may be overlooked, or broken beyond repair during extraction; it may collapse during preparation, disintegrate during storage, or, with tragic bathos, be lost.

It has been shown that the chief fossil-bearing rocks are those formed on the sea-floor. Elevation of the sediments is thus usually inevitable if their fossil-contents are to be displayed. It is possible, perhaps even probable, that isostatic crustal movements will normally raise the detrital zones along the sea-margin, sooner or later. But, whatever views may be held as to permanence of ocean basins, it is obvious that deposits formed on the floor of deeper parts of the sea are likely to reappear above its surface only very locally (in volcanic regions) or after long delay. Thus, while the coastal fauna is favourably situated in this respect, the less profuse, but no less interesting, life of the open ocean will rarely be accessible in the fossil state. Deep-sea

dredging can bring to light the existing fauna of the depths, and may even drag up samples of the soft sludge of recent deposits. But the day is far distant when mines and quarries will be opened in the rocks that underlie the ocean bed ; until then, pelagic and abysmal faunas of most past periods of geological history must remain out of reach of practical Palaeontology.

Although the greater part of the bed-rock next below the surface of the British Isles is of sedimentary origin, exposures of it are rare. Most of the country is covered, to a varying and often great depth, with the disintegrated rock-waste known as "drift." Even if such a Herculean feat were possible, removal of this superficial layer would evoke violent protest from farmers, botanists, and all other terrestrial animals ; moreover, it would result in their prompt extinction. Nevertheless, many geologists and all Palaeontologists must sympathize with the Walrus and the Carpenter in their distress at the mask of drift that covers the face of the Earth. Only along sea-cliffs, in hilly regions where the soil creeps down from the slopes, or along the courses of torrents, is the bed-rock laid bare by natural agents. Meagre though these natural outcrops of rock may be, they are more persistent, and often individually more extensive, than the artificial excavations made in railway cuttings, sewer-trenches, quarries, mines or borings. A railway cutting is dug out once for all (often by the soulless agency of a steam-navvy), and it is usually to the company's interest to obscure the sides of the permanent way by "sloping" and plantation. Quarries are, for the most part, small and temporary ; with increasing facilities of transport, drawing of stone tends to become centralized in favourably situated localities (not selected for their geological interest or fossiliferous nature), and small local stone-pits soon become degraded.

Mines, other than coal-mines, are rarely driven in fossiliferous rocks, while borings are usually so small in diameter that the cores (if any are raised) cannot include much fossil evidence. Unlike many metallic ores, fossils do not tend to increase in abundance near the surface, so that it may be assumed that the vast majority of fossils are as yet not only uncollected, but inaccessible.

The ruthless tools of denudation, which may carve out fossils from their matrix, are not content with that beneficent work; they will not rest until the organic remains, as well as the rock containing them, are shattered or dissolved. Much of this destruction is carried out beneath the mantle of drift, so that fossil evidence is destroyed just when its appearance seemed imminent. Weather beats continually against exposed rock-surfaces; blows from geological hammers are few and intermittent. For one fossil that is found "weathered-out," scores have been weathered away. These are disasters beyond human control; but the case is scarcely better when artificial processes excavate the rocks. The average quarryman or miner usually picks out, and possibly cherishes, large or otherwise striking specimens; but he has neither the time nor training to search for less obvious fossils, nor, usually, to keep sufficient record of the horizons from which his picked samples have come. Most quarried material is transferred direct to lime-kilns or stone-crushers, and its included fossils are as lost to Palaeontology as if they had never existed. Only those specimens that happen to be exposed on the occasions of rare and hurried visits by "fossil-hunters" are likely to be saved; much of the evidence that these can supply may be lost if the collectors are among the uninitiated. An attempt is made in Chapter III. to indicate the methods to be employed in collecting fossils so that their full value can

PLATE I

FIG. 1

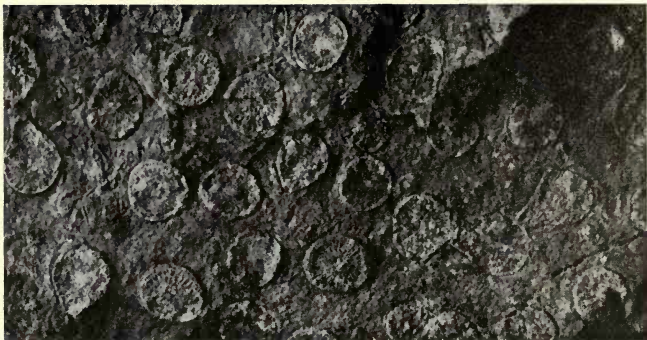


FIG. 2



FIG. 3





FIG. 1

PLATE I

FIG. 1. Block of Carboniferous Limestone containing *Lithostrotion irregulare*. Port St. Mary, Isle of Man.

FIG. 2. Block of Carboniferous Limestone composed of columnals of *Actinocrinus*. Castleton, Derbyshire.

FIG. 3. Block of Bathonian Limestone composed of *Millericrinus*. Lansdowne, near Bath.

FIG. 2



FIG. 3

PLATE I

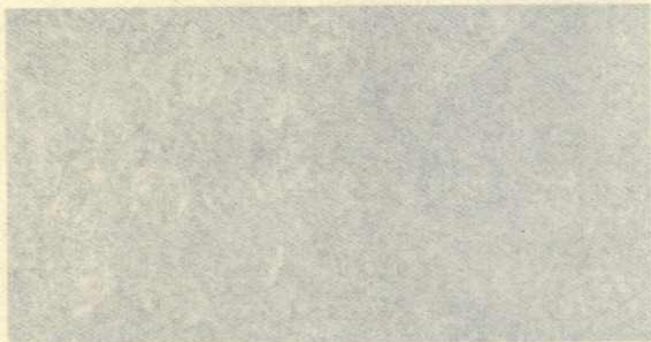


FIG. 1

PLATE II

- FIG. 1. Block of Ludlow (Aymestry) Limestone composed of *Conchidium knighti*. Weo Edge, Shropshire.
- FIG. 2. Nodule of Flint from the Upper Chalk, containing, and derived from, *Ventriculites*. Peppard, Oxon.
- FIG. 3. Block of Bembridge Limestone (Oligocene), largely composed of *Limnaea* and *Planorbis*. Bembridge, Isle of Wight.

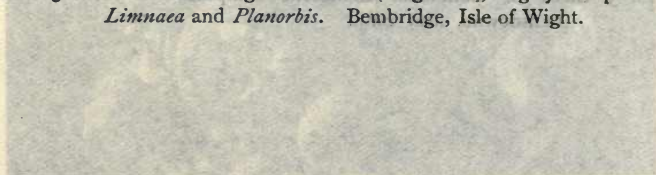


FIG. 2



FIG. 3



FIG. 1

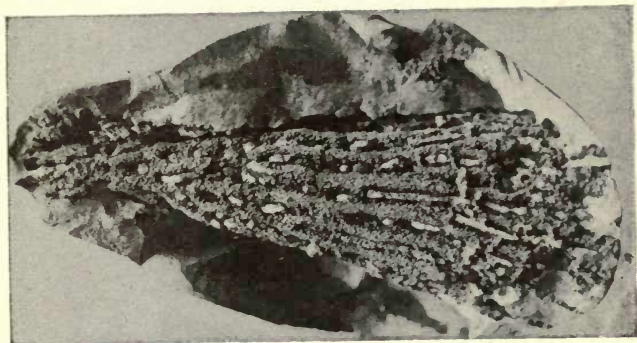
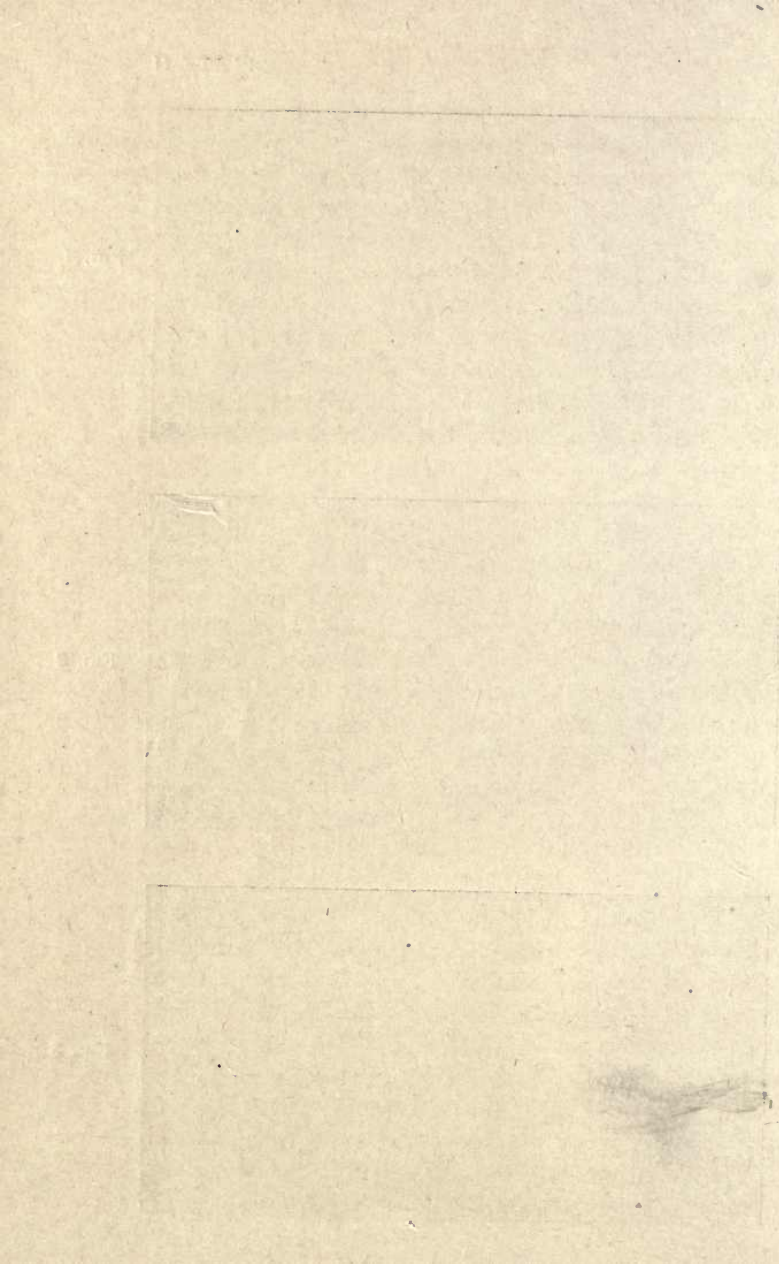


FIG. 2



FIG. 3



be retained. But if the foregoing gloomy, though not unduly pessimistic, sentences should induce a few more lovers of Nature to preserve any fossils they see, the main purpose of this book will have been achieved. A man who finds an ancient inscription or roll of papyrus, lying in a place where destruction is inevitable, and who leaves it to decay, is hardly less a vandal than one who deliberately destroys it. The history of the Earth and its inhabitants is a wider problem than that of merely human progress. The documents are less complete, and most of them must needs perish unread. Those that can be saved must be rescued at the first opportunity. With fossil-collecting it is always a case of "now or never."

Every fossil, then, should be an object of veneration. However imperfect or obscure it may be, it is a representative of hundreds, perhaps thousands, of organisms whose remains were not preserved, or will never fall into human hands. Let those hands deal gently and reverently with such as have survived risks innumerable to give their fragment of testimony on the history of Life!

(B) THE OCCURRENCE OF FOSSILS

(I) FOSSILIFEROUS AND UNFOSSILIFEROUS ROCKS

The three rock-types that make up the bulk of the Earth's crust are described, from the modes of their formation, as Igneous, Metamorphic and Sedimentary. The first type is the product of consolidation of Magma, a complex mineral solution that can be developed only at considerable depths. When solidification takes place underground, the rocks formed cannot be expected to contain any traces of life. But when magma is extruded as lava, it may occasionally catch up organic remains

(among other *débris*) and enclose them on crystallization. Such a process usually results in utter destruction of organic matter; but sometimes the lava consolidates before the whole fabric is consumed, thus perpetuating an impression of its form. Even ears of corn have been found "fossilized" in recent lava-streams. However, occurrences of this nature are so rare that magmatic rocks may be dismissed as practically unfossiliferous.

The products of volcanic explosion fall into a different category. While coarse blocks of agglomeratic material are likely to crush organisms beyond recognition, the finer "ash" or tuff settles so gently (especially under water) that it is no more destructive than clay or ooze. Since most tuffs that are geologically persistent are those erupted under, or carried into, the sea, they resemble sedimentary rocks in accumulation, and hence may include fossils. Although the immediate vicinity of a volcanic vent would soon become destitute of life, regions far removed from the danger-zone receive great quantities of fine ash, transported peaceably by currents. Thus, while tuffs associated with agglomerates and lava-flows are usually barren, those interbedded with ordinary sediments are often fossiliferous.

Metamorphic rocks result from recrystallization of other types under the influence of heat or crustal movement. Even those schistose varieties whose sedimentary origin is probable have undergone much molecular readjustment, so that the original character of the rock and its contents is altered. But metamorphism varies in degree, and such rocks as clay-slates, in spite of cleavage and incipient crystallization, often contain recognizable traces of organic remains. These are usually much distorted (see Pl. iii. fig. 3); indeed, the state of the fossils was one of the phenomena that proved the tectonic origin of slaty cleavage. As a

general rule, metamorphic rocks are unfossiliferous. This is doubtless one of the chief reasons for our sparse knowledge of ancient faunas, since the older rocks have been involved most frequently in metamorphic stress.

There remain the sedimentary rocks, in which alone organic remains can be reasonably expected to occur. As has been shown in a previous section, the three types, arenaceous, argillaceous and organic, vary in quality as matrices for preservation of fossils. Sands may be terrestrial in origin (like some of the Old Red and many Triassic sandstones), and will then prove scarcely fossiliferous—owing partly to the paucity of life in deserts, and partly to the imperfect burial afforded. Coarse breccias or conglomerates are rarely fossiliferous; such organic remains as they enclose are usually in poor repair. Fine-grained sandstones are often replete with fossils (*e.g.* the Caradocian of Shropshire or the Thanet Sands), but very little exposure to weathering reduces the remains to the state of casts.

Clays and shales, which afford the best matrices for preservation, are by no means always richly fossiliferous. The Wenlock Shales, Liassic clays, Gault and Barton Beds may be cited as argillaceous deposits in which, locally at least, rich “hauls” may be expected. But against these must be placed the Old Red Marls of Herefordshire, the Keuper Marls, much of the Weald Clay and the Reading Beds. The scarcity of invertebrate fossils in these rock-systems is probably due in large measure to the terrestrial, lacustrine or deltaic conditions of their formation. The moral to be drawn from the comparison is that *mottled* clays are rarely rich in fossils. This is well illustrated in the Wealden of the Isle of Wight, where grey-laminated clays are crowded with *Cypridea* and *Cyrena*, while associated mottled beds are practically barren. Argillaceous rocks are specially

liable to metamorphism, but the contortion and cleavage that have confused such systems as the Longmyndian or Manx Slates seem insufficient reasons for their unfossiliferous nature. Other greywackes, in much the same condition, contain traces of organisms, obscure though they may be. The barrenness of the vast piles of argillaceous Pre-Cambrian strata demands a further explanation.

Typical limestones are largely built of organic remains, but this does not prevent them from often disappointing collectors of macroscopic fossils. Not only does the similarity in mineral composition between matrix and shell make their separation difficult and fortuitous, but often large fossils are wholly wanting. Unless the limestone has undergone marmorosis or dolomitization, a microscopic section will usually reveal foraminifera or shell-fragments, but even such apparently promising strata as the Coralline Oolite or Upper Chalk may prove destitute of separable fossils through a weary succession of exposures. Limestones of relatively littoral origin are usually more prolific than oozes, so that the best fossil-hunting is to be found in such deposits as the Silurian, Carboniferous and Jurassic Limestones. Among siliceous rocks, radiolarian chert rarely includes many fossils apart from the Radiolaria themselves, while chert derived from dissolution of sponge-spicules may contain abundant remains of larger organisms, usually as casts or siliceous petrifications. Carboniferous and Portlandian cherts are familiar examples of such rocks.

Peat is often crowded with shells of fresh-water mollusca, but these rarely remain in carbonaceous rocks approaching coal in constitution. The organic acids produced by plant-decay speedily remove calcareous structures. Although molluscs and other Invertebrates are occasionally found in cannel, they are almost always

represented by obscure impressions. It is only in associated shales, or in mineral concretions, that the Invertebrate fauna of the Coal Measures is adequately preserved.

(II) FOSSILS AS ROCK-FORMERS (Pls. i. and ii.)

Organic rocks, as their name implies, consist of matter that owes its solidity and form to the influence of living beings. The mineral substances most abundantly secreted by Invertebrates are Calcium carbonate and phosphate, and colloid Silica. Since these minerals are readily soluble in crustal water, considerable molecular rearrangement is bound to supervene in rocks built of them. Hence the organic origin of a rock does not automatically imply persistence of recognizable organic remains. Solution and re-deposition of Calcite, and conversion of opal into Chalcedony, will entirely obliterate small shells, and destroy the finer features of larger ones. The most extensive and massive deposits of calcareous and siliceous rock are the oozes, whose chief constituents are small Protozoa. In such deposits as Chalk or Barbados Earth, Foraminifera and Radiolaria, however minute, are in preservation equal to that of modern ooze-formers. But in limestones of the texture of the Carboniferous Limestone, or cherts like those of the Scottish Ordovician and Devonshire Culm, Protozoa are usually scarce and indistinct. It is noteworthy that the few Foraminifera known from Palaeozoic rocks are, on the whole, larger than those characteristic of more recent deposits; while the surviving Radiolaria in Culm-Measure cherts are often distinguishable with the naked eye. This suggests that the smaller organic remains of ancient deposits have disappeared during molecular readjustment, and that Protozoan oozes may actually have been as abundant in Palaeozoic times as

they are to-day. Apart from the Chalk, there are few such rocks in the British sequence, although *Saccamina* in the Carboniferous, and *Nummulina* in the Eocene, often give character to the beds in which they occur.

The majority of Siliceous sponges, in spite of their large size, collapse after death into a welter of slender spicules, whose fate is normally like that of Radiolaria. Some Lower Cretaceous cherts contain visible evidence of the Poriferan origin of their silica, while the flints in Chalk must have been derived largely from dissolution of sponge-spicules (Pl. ii. fig. 2). Calcareous sponges are more massive and durable; some bands in the Inferior Oolite, and the Aptian of Faringdon, are largely built of their remains.

The reef-building capacities of Corals are well known, and Madreporaria (or allied Coelenterates of similar habit) have produced limestones at several stages in British geological history. It must, however, be remembered that a coral-reef is rarely built solely of corals, while a large proportion of those animals are not reef-makers. The colonial masses, and their broken fragments, constitute much of a typical reef, but members of other Invertebrates that sheltered in the wall, or became involved in its ruins, form a considerable bulk. Calcareous algae have no small share in reef-construction. The chief limestones in Britain that contain reef-building corals are the Wenlock, Devonian and Carboniferous Limestones (Pl. i. fig. 1) in the Palaeozoic, and local beds in the Lower Oolites and Corallian in the Mesozoic.

Among Echinodermata, the Crinoidea secrete the most massive and extensive skeletons; groups prevalent in Palaeozoic times were especially remarkable for this quality. Parts of the Wenlock and Ludlow Limestones, patches of Devonian "marbles," and important masses

of the Carboniferous Limestone (Pl. i. fig. 2), are replete with Crinoid columnals almost to the exclusion of other material. In Mesozoic rocks remains of Crinoids are often abundant, but they are rarely so profuse as to make up much bulk of the strata in which they occur. Thin sheets of sparry limestone in the Lower Lias, representing individuals or clusters of *Pentacrinus*, and beds of *Millericrinus* in the Bathonian (Pl. i. fig. 3), afford exceptions to this general rule. Echinoids, though often common fossils, never attain the rank of rock-formers in this country.

The flimsy colonies of calcareous Polyzoa are often abundant, but it is rare to find them in the rôle of rock-formers. *Fenestella* sometimes crowds layers of Carboniferous and Permian Limestones; while more massive "Corallines" are important constituents of the Faringdon Greensand and Pliocene Crags.

Brachiopoda flourished to such a degree in the shallower Palaeozoic seas that they rank as the chief "shells" of that epoch. In consequence, the equivalents of modern shell-beaches were made of their remains. Various members of the Orthacea convert some layers of Ordovician sandstone into local limestones, *Pentamerus* does the same in the Llandoverly, *Leptaena* and *Atrypa* similarly constitute parts of the Wenlock, while *Conchidium* is largely responsible for the existence of the Ludlow Limestone (Pl. ii. fig. 1). Many masses of Devonian Limestone are replete with Brachiopods of various genera, while the broken shells and spines of *Productus* give character locally to the Carboniferous Limestone. In later periods Brachiopods were, on the whole, less numerous, though certain genera of Rhynchonellacea and Terebratulacea give a distinctive appearance to some Jurassic Limestones, and constitute no small proportion of their bulk.

After the Palaeozoic epoch, Mollusca assumed the mantle of the Brachiopoda. In particular, the Ostreidae, which even to-day occur in congested clusters round our shores, are responsible for much of the Middle Lias of Yorkshire and the Forest Marble of the Southern Counties. Ammonites are rarely rock-formers, but at some horizons in the Inferior Oolite of Dorsetshire (*e.g.* at Burton Bradstock and Bradford Abbas) they are so abundant that the scanty matrix scarcely separates the shells. In Tertiary times, Molluscan life in the British area was rarely of such exuberance as to mask the character of the sediments, but the well-known Oyster-bed at the base of the Reading series, the "basement-bed" of the London Clay, layers in the Bracklesham and Barton series, the Oligocene (Pl. ii. fig. 3), and parts of the Crag, owe much of their bulk to the abundant Pelecypoda and Gastropoda.

Trilobites are often disseminated (in a more or less broken state) in great profusion in Lower Palaeozoic rocks, and even in the Carboniferous Limestone, but they can hardly be classed as rock-formers. The most efficient Arthropoda in this respect are the Ostracoda. *Beyrichia* in the Ordovician and Silurian, and *Cypridea* in the Wealden, often occur in swarms to the virtual exclusion of matrix; but their small size and impersistent deposition restrict their rock-forming capacities to thin beds. Examination of prepared "flint-meal" shows abundant Ostracoda in the Chalk ooze; their remains are usually subordinate to Foraminifera and Spongespicules.

(III) FOSSIL-BANDS (Pl. vi.)

Brief experience of fossil-hunting suffices to show that organic remains are rarely scattered evenly through a deposit, but tend to occur in more or less defined bands.

In most cases restriction of fossils to thin, often imper-sistent, layers is not associated with any marked changes in the matrix. Even so homogeneous a rock as the Upper Chalk may show discontinuity in its fossil contents, but the feature is most common, and most striking, in littoral or shallow-water deposits. The Ordovician rocks of Shropshire illustrate the phenomena in a remarkable manner (Pl. vi. fig. 2). The more arenaceous portions, such as the Horderley Sandstone or Acton Scott Beds, consist of alternations of hard, flaggy sandstone almost devoid of fossils, with thin, impure lime-stones (becoming "rotten" on weathering) in which fossils are so crowded that detrital matter is subordinate. Again, the Onny Shales are famed for their abundant *Trinucleus*; but, unless the right layer is located, search will be scantily rewarded. The Upper Silurian rocks of the same district show similar qualities. Matted layers of *Orthis* and *Chonetes*, only one shell thick, are separated by considerable masses of sparsely fossiliferous Upper Ludlow flags (Pl. vi. fig. 1), while the comparably congested band of *Lingula cornea* that underlies the Old Red Marls is isolated in a great bulk of barren micaceous sandstones. Mention may be made of the classic "Ludlow Bone Bed," where Vertebrate remains occur under similar conditions. In rocks of much later formation the same feature is found. Visitors to White-cliff Bay, in the Isle of Wight, can hardly fail to notice the thick layer of white shells (chiefly *Cardita* and *Turritella*) which stands vertically in the cliffs of dark Bracklesham clay; closer inspection shows that fossils of the Tertiary deposits in the island are usually disposed in bands.

It is difficult to give a general explanation of this phenomenon; each case will have its determining causes, and these may or may not be apparent. However, it

is possible to discriminate between fossil-bands due to the mode of life (or manner of death) of the organisms concerned, and those produced by physiographical agents working on discarded shells. As a rule, the former types consist of well-preserved specimens of a single species, while the others include a variety of more or less damaged fossils.

The local and congested habits of life of many sedentary Invertebrates are illustrated by the familiar mussel and oyster beds of British shores. Dredging in deeper water proves that large areas of the sea-floor below low-tide mark may be covered with *Pecten* or *Echinus* to the virtual exclusion of other types. Moreover, it is by no means uncommon to find that the dredge brings up nothing, or dead shells only, from a place that yielded a rich harvest of living specimens at a previous haul. Those Invertebrates that lead more or less sedentary lives when adult, but have free-swimming larval stages, are apt to congregate into clusters whose situation changes periodically, perhaps with each generation. The evidence available indicates that Echinoderms, Brachiopods and Pelecypods often show these habits, in coastal or deep water. In a region where rock-deposition is in progress, it is easy to account in this way for inclusion of layers composed of one or two species of shells in sediment which, above and below, contains few of their remains.

Again, if some rapid or cataclysmic change occurs in the surroundings of a faunal assemblage, sudden death will overtake all those incapable of speedy escape. Such disasters are not likely to come frequently, but they may occasionally overwhelm inhabitants of coastal regions. Sudden outpouring of mud from a river in flood might smother organisms unable to swim, and rapid shifting of sand-shoals in a storm would have a like effect.

Earthquakes and volcanic eruptions would hardly work such havoc upon Invertebrates as they often produce among fishes; but if they caused upheaval or other geographical changes, their sudden nature would be fatal to sedentary forms. It is possible that some of the fossil-bands of the uppermost Silurian, notably the Bone Bed and *Lingula*-bed before mentioned, may be due to seismic catastrophes.

The clearest and most frequent types of fossil-bands are found in strata of the littoral zone. In most of such cases the shell-beds contain a variety of forms, although one or two species usually predominate. Almost all the fossils are worn or broken, and the matrix may be full of shell-fragments. These fossil-bands can be ascribed to tidal currents or waves, sorting out dead shells of similar shape and weight, and drifting them to the beach or sheltered water. "Shell-sand" is a common product of this action. On sandy beaches it is quite usual to find abundant shells after continued winds from a particular quarter, while at the next visit nothing but sand and shingle can be seen. If isostatic conditions are such that permanent sedimentation is in progress, such episodes will be perpetuated as alternations of fossiliferous and barren deposits.

Lastly, reduction in the rate of accumulation of sediment, due to conditions that do not seriously affect the local fauna, naturally increases the relative number of fossils in a given mass of rock. Development of organic oozes on the floor of the open sea, beyond detrital limits, gives an extreme example of this type of "fossil-band." Local (usually temporary) circumstances may give comparable results in coastal deposits. Illustration of such conditions is found in the Inferior Oolite. In Dorsetshire, where, owing to irregularity and hindrance in isostatic depression, rocks of this system rarely exceed

twenty feet in thickness, fossils of many kinds are so crowded as to be almost in contact. In Gloucestershire, where depression allowed accumulation of sediment reaching two hundred feet in thickness, fossils are generally more widely separated. There is no reason to suppose that the abundance of life was seriously different in the two districts at any time in the Inferior Oolite stage; the apparent difference is due to the amounts of sediment in which the fossils are embedded. The fossiliferous character of the Chalk Rock, and lower parts of the Upper Chalk, in the South of England, is a further example of this phenomenon.

(IV) NODULES (Pl. ii. fig. 2; Pl. iv. fig. 1)

Concretionary structures are characteristic of many sedimentary rocks, especially argillaceous types. Concretions differ in composition and origin, but they agree in being developed after accumulation of the sediment. Calcium carbonate, ferrous carbonate and opaline Silica are frequently present in clays and limestones. Their ready solubility in surface water ensures removal from exposed layers, while their relative insolubility in non-aërated water encourages precipitation at greater depths. Petrification often results from differential solubility, but formation of concretions is perhaps more usual. In some deposits, such as the Old Red Marls of Herefordshire, the Lower Liassic clays of Dorsetshire, or the Upper Chalk, calcareous or siliceous ingredients have segregated into apparently "sedimentary" sheets of Cornstone, Cement-stone and Flint. In others, such as the Coal-Measure shales, the Upper Lias of Yorkshire (Pl. iv. fig. 3), or the London Clay, Ironstone, Cement-stone or Septarian nodules are developed. Precipitation of dissolved minerals is assisted by, and usually centred around, some particle of solid matter with similar

crystalline properties. Thus the nucleus of a chalybite or calcareous nodule is often a calcite shell, while that of a flint-nodule is usually a siliceous sponge. Although the fossil causing the nodule may have been a mere fragment, it is usual to find organic remains in concretions better preserved than those in the surrounding rock. The superior hardness and impermeability of the subcrystalline material give protection to its contents. Thus in the Lias of Whitby, Ammonites in nodules are often perfect in form and detail; while those in the shale are flattened almost beyond recognition. Similarly, Sponges in the Chalk (Pl. ii. fig. 2) are represented by obscure impressions, save for those encased in flint. In the latter case, spicules, and ooze-forming organisms mingled with them, can be picked from the "flint-meal" perfect and unchanged.

Marcasite and Pyrites are often deposited in crystalline masses around fossils buried in clay. Commonly the enclosed organisms have been petrified by the mineral, precipitation continuing after replacement was complete. More rarely the original shell is retained with an incrustation of Iron Pyrites showing a rough indication of the form of the fossil (Pl. v. fig. 2). Such nodules are not satisfactory from the palaeontological standpoint, since the hardness of the crust, and its liability to decay with liberation of sulphuric acid, make extraction and preservation of the contents difficult or impracticable.

(V) DERIVED FOSSILS

Sedimentary rocks are built of the ruins of others. The materials employed may have formed part of igneous, metamorphic or older sedimentary rocks. The ruins of a sedimentary rock are likely to include some of its enclosed fossils. Hence it follows that fossils

representing a fauna long past may be reinterred among shells of a later period. In the palaeontological record, as in human manuscripts, "anachronisms" may occur; but they can only be retrospective in character, and so would be more accurately termed "Catachronisms." Fossils derived from denudation of older rocks are unlikely to be found in any but littoral deposits, and even there can be confidently ascribed to local origin. During degradation of a sea-cliff, many fossils will fall to the beach, but the scour of waves will destroy all that are not speedily buried in sand. Of the innumerable fossils "weathered out" on a land surface, few, if any, survive the dangers of travel to a place of permanent sedimentation. Glaciation may, however, transport shells unharmed for great distances, as is shown by the frequent occurrence of *Gryphaea* and other massive fossils in the Boulder Clay.

Conglomerates, such as the Budleigh Salterton Pebble bed, may include pebbles that are fossiliferous, but under such circumstances there is little risk of confusion. However, many layers in the Dorsetshire Inferior Oolite and East Anglian Pliocene are remanié beds made up of fossils separated from their matrix. Again, the Lower Greensand of Faringdon and Cambridgeshire contains many Belemnites and other durable fossils that are not Aptian, but Kimmeridgian. The normally broken and water-worn nature of such truly "extraneous" fossils is not a reliable criterion of derived origin; wave-action can produce such conditions in a few hours. Only by careful identification and comparison can the true fossil evidence be sifted from the false. But derived fossils, though deceptive in some respects, are of great geological interest, since they indicate the age of the rocks locally exposed to denudation at the period in whose sediments they occur.



PLATE III

FIG. 1. *Trigonis clavatus* with the ligament preserved. Corallian, Weymouth.

FIG. 2. *Trigonis turgida*. Internal mould. Portlandian, Swindon.

FIG. 3. *Arachnia subrotunda*. Moulded by clay. Portlandian slate, Mendips, N. Wales.

FIG. 4. *Trigonis turgida*. Rhynchonellid. The pyramidal shell is external.

FIG. 5. *Trigonis turgida*. Rhynchonellid. The pyramidal shell is internal.



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PLATE III

- FIG. 1. *Trigonia clavellata* with the ligament preserved. Corallian, Weymouth.
- FIG. 2. *Trigonia incurva*. Internal mould. Portlandian, Swindon.
- FIG. 3. *Angelina sedgwicki*. Distorted by cleavage. Tremadoc slates, Minfford, N. Wales.
- FIG. 4. *Glycimeris glycimeris*. Pliocene, Suffolk. The aragonite shell is crumbling.
- FIG. 5. *Ostrea edulis*. Pliocene, Suffolk. The calcite shell is in perfect preservation.

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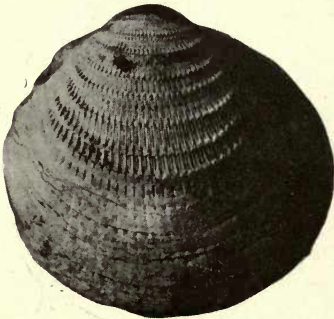
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(C) THE PRESERVATION OF FOSSILS

(I) COMPLETE OR UNCHANGED PRESERVATION

The soft tissues of Invertebrates are of such texture that their preservation, even for short periods after death, requires rapid and exceptional processes. Such processes are likely to develop protective matrices which are themselves doomed to decay. Whereas plants may grow in such profusion that their matted remains exude antiseptic fluids sufficient to prolong the existence of cell-contents (thereby giving opportunity for more perpetual preservation), animals rarely congregate, either in life or death, in masses comparable with peat. Even in coral-reefs the polyps are separated by disproportionate quantities of mineral matter incapable of retarding the chemical dissolution of its builders. Few Invertebrates have tough "skins," although the ligaments of Pelecypoda have merit in this respect. Such ligaments are occasionally preserved (with but slight shrinkage or carbonization), and may be found in rock-systems as far back as the Jurassic (Pl. iii. fig. 1). They are most often met with in clays or rocks with much argillaceous content, and are perhaps least rare in the Dorsetshire Corallian and London Tertiaries.

The most perfect type of preservation is found in masses of amber that enclose small insects. The sticky resin that may entangle and enshroud organisms can do so only when freshly extruded, and so is available for aseptic preservation of terrestrial or aerial forms alone. Since amber is bound to undergo gradual carbonization, the beautiful and effective mode of fossilization that it lends to types of Invertebrates otherwise rarely preserved can be but temporary; such evidence does not extend back beyond the Tertiary stage.

Specimens of fossiliferous amber, probably derived from older deposits, are occasionally found in the East Anglian Pliocene and Pleistocene.

The shelly structures of fossil Invertebrates are commonly found in a condition hardly different from those of living forms. Usually, however, complete removal of the encasing and penetrating organic tissue renders "desiccated" shells very friable. Since solution or replacement are inevitable for shells exposed to the action of water, clays or nodules supply the only matrices in which unchanged preservation can be long maintained. Even in such surroundings the nature of the shell-substance influences the permanence of the fossil. Calcite may retain its original characters so perfectly that its pearly lustre (and even traces of coloration) may be found in deposits as old as the Lias. Even in the porous sands of the Crag, *Ostrea* persists unchanged. But Aragonite can rarely escape removal or alteration, whatever may be the character of its surrounding matrix. Comparison of figs. 4 and 5 (Plate iii.) shows the different condition of shells composed of the two forms of Calcium carbonate in the same deposit. Striking illustrations of the differing durability of Calcite and Aragonite occur in the Chalk, where large shells built of the latter (*e.g.* Ammonites and Gastropods) are represented by casts and moulds, to the walls of which adhere encrusting Polyzoa and *Spondyli* which, being made of Calcite wholly or in part, are preserved almost unchanged.

Opaline silica has considerable permanence when protected from percolating water, but it undergoes "devitrification" in time, or under influence of pressure. Chitin may remain very fresh if sealed up in a nodule or impervious clay (Pl. iv. fig. 1). The Arthropoda of the Coal Measures are but little carbonized when

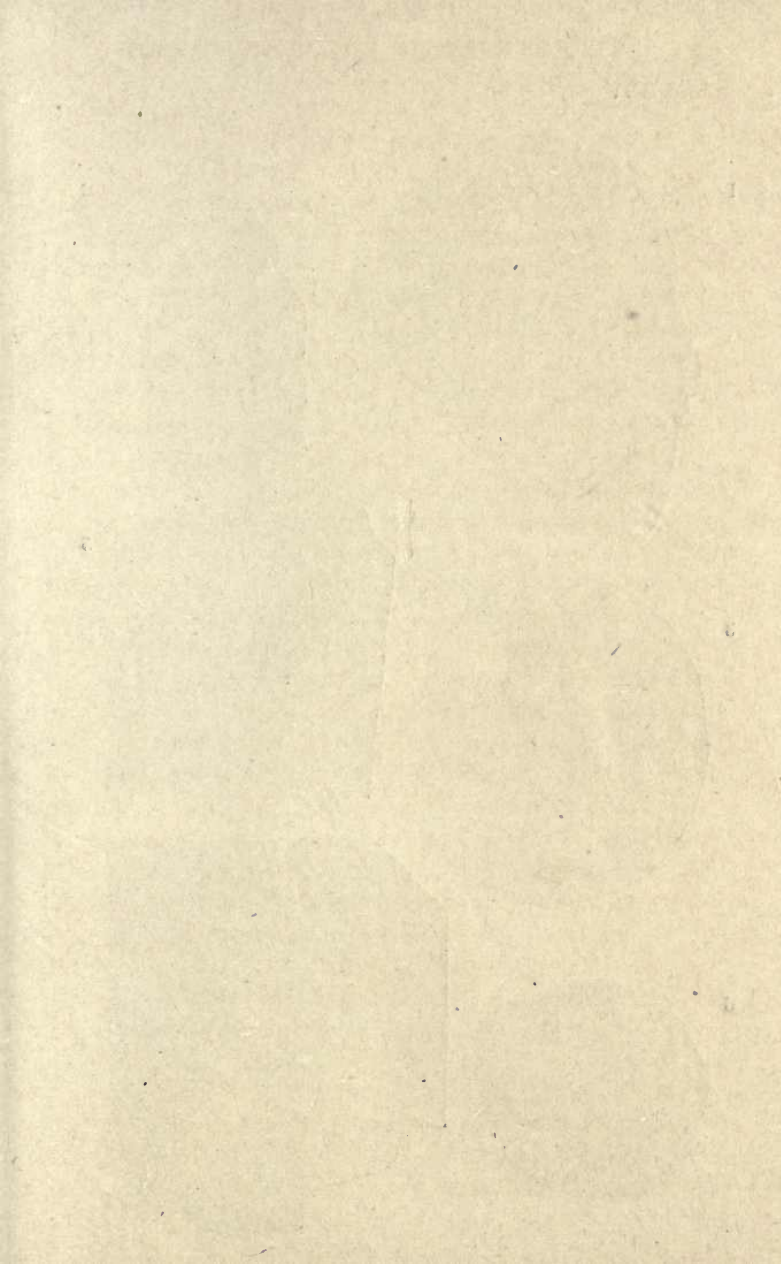


PLATE IV

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PLATE IV

- FIG. 1. *Orbiculoidea nitida*. Coal Measures, Coalbrookdale. The glossy, largely chitinous, shell is perfectly preserved in an ironstone nodule.
- FIG. 2. Fragment of Pelecypod shell from the Upper Greensand, near Sidmouth, Devon, replaced by chalcedony in the form of Beekite.
- FIG. 3. *Dactylioceras commune*. Upper Lias, Whitby, Yorks. From a nodule of cement-stone. Complete and uncompressed.
- FIG. 4. *Peronoceras annulatum* (a closely similar species). Upper Lias, Runswick Bay, Yorks. From the shale, flattened and telescoped.
- FIG. 5. *Cliona* sp. Flint moulds of the crypts perforating the shell of *Inoceramus*. Upper Chalk, Sussex.
- FIG. 6. *Atrypa reticularis*. Ludlow Limestone, West Knowle, Craven Arms, Salop. Internal mould (ventral side), showing muscular and other impressions.

Fig. 1. *Oxymonites* sp. Coal Measures, Coalbrookdale. The glossy, largely chitinous shell is perfectly preserved in an ironstone nodule.

Fig. 2. Fragment of *Pelecypod* shell from the Upper Carboniferous, near Sidmouth, Devon. The shell is chitinous in the form of

FIG. 1. *Lioceras* cf. *opalinum*. Bajocian, Burton Bradstock, Dorset.
Internal mould, showing sutures.

FIG. 2. Ammonite wholly encrusted by Pyrite and Marcasite. Oxford Clay, near Oxford.

Fig. 3. *Ceras* sp. Thin mould of the upper portion of the shell of

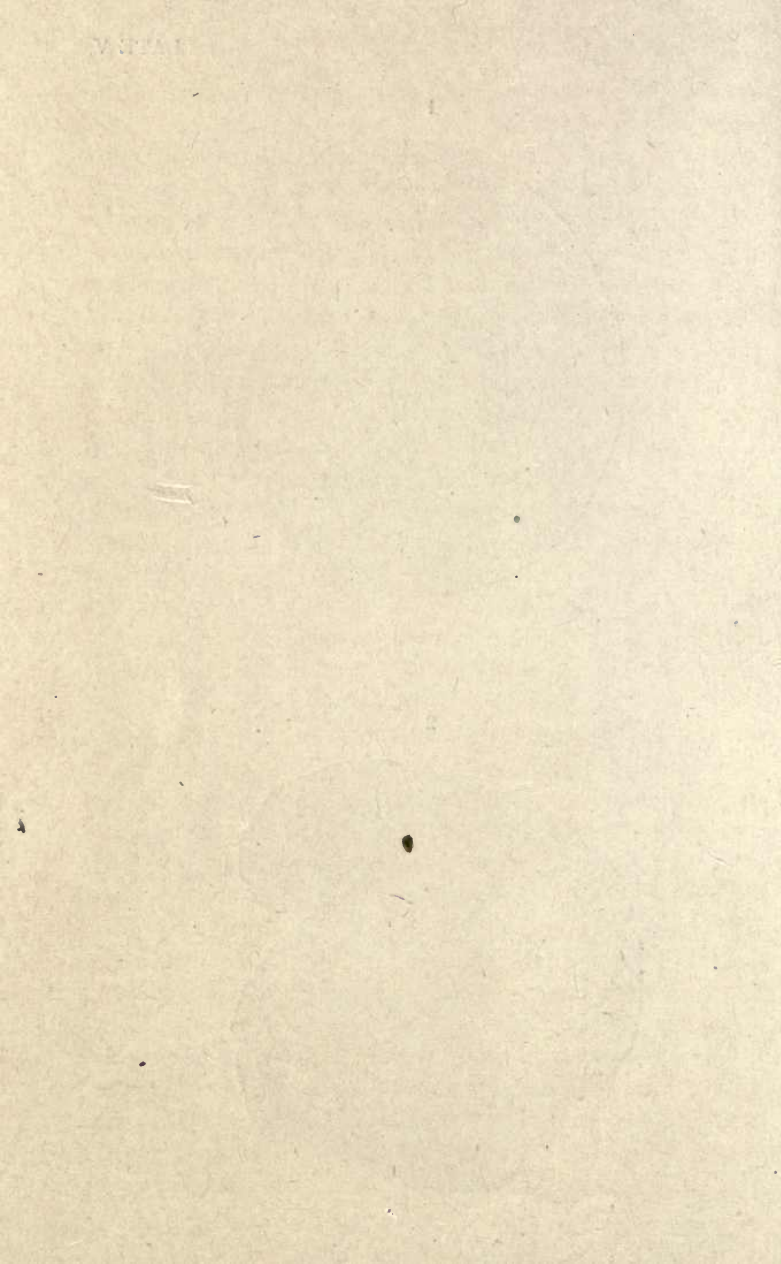
Fig. 4. *Ammonites* sp. Thin mould of the upper portion of the shell of

1



2





encased in concretions, and even Trilobites and Graptolites are occasionally found unaltered in form, and hardly changed in composition. Remarkable specimens of *Eurypterus* found in the Silurian of the Isle of Oesel (North Russia) are sometimes so perfectly preserved that the carapaces can be detached from the marl and examined by transmitted light. Lenses of compound eyes of Trilobites may also retain their transparency.

A mode of preservation in which the original tissue is retained, impregnated with fresh mineral-matter, is more usual than that indicated above, and perhaps more satisfactory on the whole. The majority of shells, and especially the skeletons of Echinoderms, have a fairly open texture, and precipitation of new mineral deposits in the pores strengthens the fabric to a degree surpassing that attained during life. Mineral impregnation is most frequent in calcite fossils embedded in calcareous matrices, and is shown most clearly in Echinoderm tests. The crystalline continuity of the fresh material with that of the original tissue may lead to disadvantages by obscuring structural outlines or inducing cleavage. The former difficulty is, however, usually mitigated by slight coloration of the secondary infilling, while the latter may be helpful in the study of tests where each ossicle is independently orientated. Occasionally the impregnating mineral may be different from that composing the test, as in fossils that are embedded in, but not replaced by, flint. Such specimens reveal minute structure with admirable definition when viewed in thin sections.

The process of infilling, which is strictly comparable with the cementation of arenaceous or calcareous rocks, may at times be carried to excess, so that incrustations of new crystalline mineral cover the surface of the fossil. This condition is particularly common in the interior of

shells or tests that were not filled by matrix, such as many Brachiopods and Irregular Echinoids. In these cases the sparry material, usually calcite but sometimes quartz, projects into the cavity and may even fill it. In Terebratulids from the Faringdon Greensand, stages in this incrustation can be traced, from a crystalline coating of the valves and brachidia to a complete internal mould, through whose transparent substance the "loop" can be seen. This style of infilling is well-adapted for preservation of the delicate internal apparatus of the Telotremata; and, thanks to the methods of preparation devised by the Rev. Norman Glass, does not prevent investigation of its structure.

Less commonly similar incrustation may develop over the external surface of a fossil. This normally obscures the finer details of ornament; but, in the case of Echinoids, it emphasizes the plate-structure by its crystalline relation to the ossicles of the test. Incrustation is normally present on the Echinoids of the Aptian of Faringdon, and sometimes occurs on those of the Chalk. In fossils from the former deposit an outer film of iron-oxide coats the excrescent calcite, and both layers may often be chipped off, leaving the unchanged test exposed.

(II) CASTS AND MOULDS (Pl. iii. fig. 2; Pl. iv. figs. 5 and 6; Pl. v. fig. 1; Pl. vi.)

In permeable rocks it is usual to find that fossils differing from the matrix in composition have been entirely removed in solution. If their removal has been postponed until the surrounding rock attained some rigidity, and if the texture of the matrix is sufficiently fine, the scars representing the missing fossils will retain, in negative, all superficial details of structure and ornament. Such negatives are termed "casts" when they

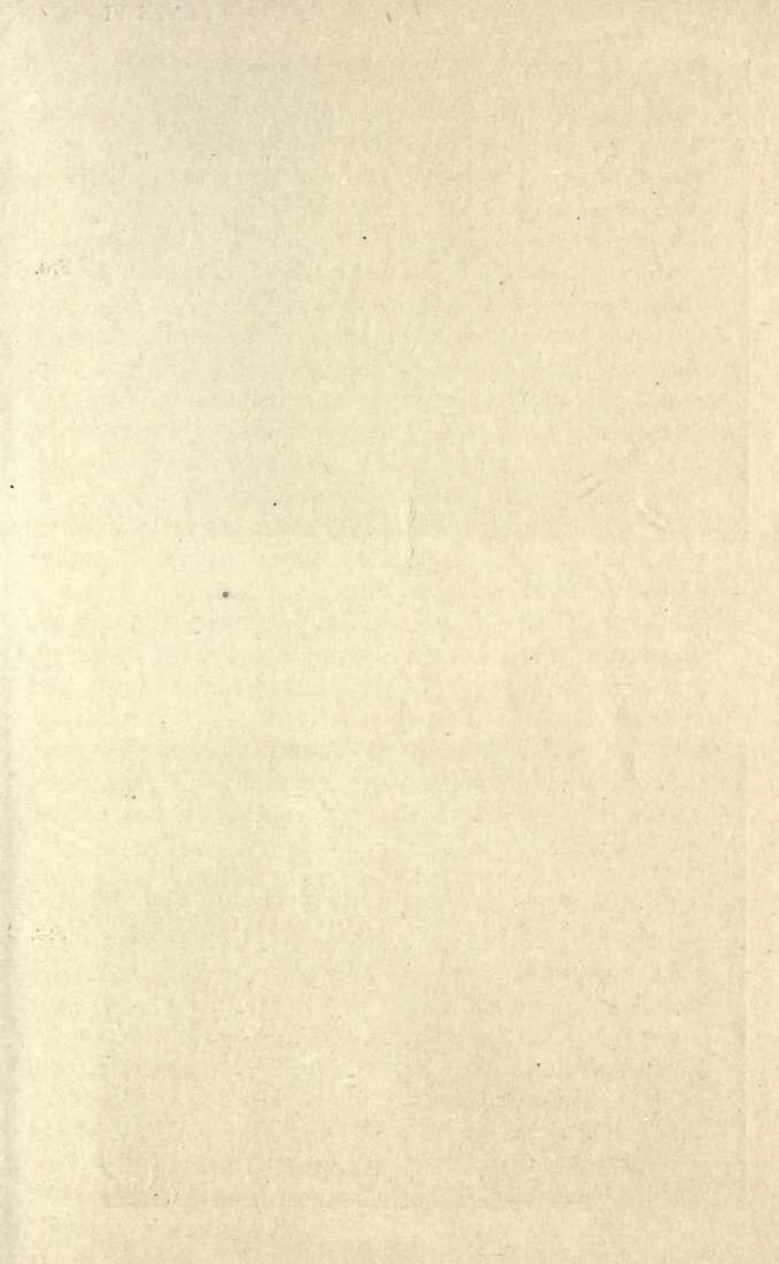




FIG. 1

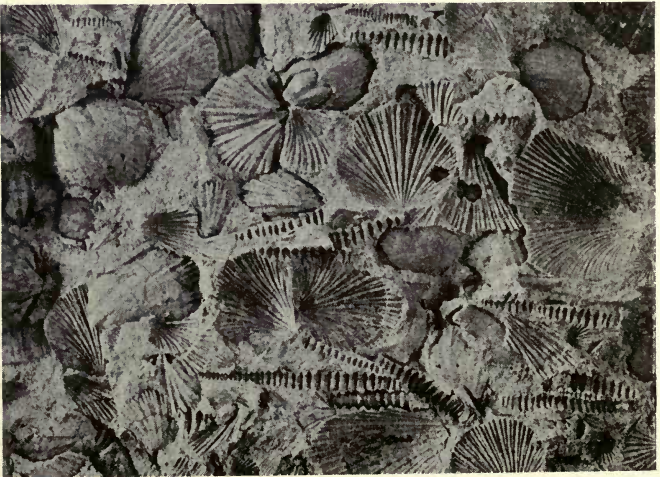


FIG. 2

are impressions of the outer surface, and "moulds" when they consist of matrix that filled the internal cavity. Clear casts are hardly inferior to preserved shells for purposes of study, since wax-squeezes will restore to positive proportions all the surface characters of the dissolved fossils; while moulds are, in many cases, far more instructive objects than perfect shells. It is exceedingly difficult to dissect out the hinges or muscle-impressions of Pelecypoda or Brachiopoda set in refractory matrix, but the full structure of these internal features can be examined on moulds, or on artificial positives taken therefrom. Indeed, so useful are natural moulds in this respect, that many methods have been devised

PLATE VI

FIG. 1. Part of a fossil-band in Upper Ludlow Flags, Onibury, Salop. The right-hand side was near the quarry-face, and solution has reduced the organisms to casts and moulds. Farther in (to the left of the figure) the shells are preserved intact. "*Orthis*" *lunata*, *Chonetes striatella*, and *Camarotoechia* sp. are the chief forms present.

FIG. 2. Part of a fossil-band in Caradocian (Acton Scott beds), Marshbrook, Salop. Completely decalcified. "*Orthis*" *testudinaria* and *Tentaculites*. while the Portland Oolite is a well-known example of a similarly carious limestone. As a general rule, this style of preservation represents all kinds of fossils in arenaceous or cherty rocks, while in calcareous matrices fossils of aragonite and opaline silica are usually indicated by negatives.

Under conditions of slow or intermittent deposition, empty shells may become filled with concretionary matter differing from the matrix by which they are subsequently surrounded. The shells themselves are often removed before burial is completed, so that moulds, without casts, are the sole relics of the organisms. Glauconite is often found in grains representing cavities of Foraminiferal chambers, while impure phosphate of lime ("coprolite") similarly occurs as con-

FIG. 1

FIG. 1. Part of a fossil-bed in Upper Lias (Gumbert, Salop). The right-hand side was near the quarry-face, and solution has reduced the organisms to casts and moulds. Farther in (to the left of the figure) the shells are preserved intact. "*Ostrea*" *imula*, *Chonetes striatella*, and *Camartoechia* sp. are the chief forms present.

FIG. 2. Part of a fossil-bed in Caradocian (Aston Scott beds) Marshbrook, Salop. Completely decalcified. "*Ostrea*" *asturiana*

FIG. 2

are impressions of the outer surface, and "moulds" when they consist of matrix that filled the internal cavity. Clear casts are hardly inferior to preserved shells for purposes of study, since wax-squeezes will restore to positive proportions all the surface characters of the dissolved fossils; while moulds are, in many cases, far more instructive objects than perfect shells. It is exceedingly difficult to dissect out the hinges or muscle-impressions of Pelecypoda or Brachiopoda set in refractory matrix, but the full structure of these internal features can be examined on moulds, or on artificial positives taken therefrom. Indeed, so useful are natural moulds in this respect, that methods have been devised for the artificial removal of preserved shells, with intent to reveal internal structures impressed on the infilling matrix. Fig. 2, Pl. iii., and fig. 6, Pl. iv., show how admirably the features of fossils may be represented by this mode of "destructive preservation."

The fine sandstones of the Shropshire Ordovician contain "rotten-bands" caused by innumerable casts and moulds (Pl. vi. fig. 2), while the Portland Oolite is a well-known example of a similarly carious limestone. As a general rule, this style of preservation represents all kinds of fossils in arenaceous or cherty rocks, while in calcareous matrices fossils of aragonite and opaline silica are usually indicated by negatives.

Under conditions of slow or intermittent deposition, empty shells may become filled with concretionary matter differing from the matrix by which they are subsequently surrounded. The shells themselves are often removed before burial is completed, so that moulds, without casts, are the sole relics of the organisms. Glauconite is often found in grains representing cavities of Foraminiferal chambers, while impure phosphate of lime ("coprolite") similarly occurs as con-

temporaneous moulds of larger shells. The Cambridge Greensand, "Chloritic Marl," and rock-bands of the Chalk include good examples of this phenomenon; while the pyritous moulds of Liassic Ammonites and flint moulds of Cretaceous Echinoids are somewhat analogous.

(III) PETRIFICATION

(a) *By infilling*

Fissures and other open spaces in rocks tend to become clogged by precipitation of "vein-minerals" brought in solution by water. The cavities separating casts from moulds are thus liable to be filled by new mineral matter. This will usually be different from that originally composing the fossils, and normally less soluble. Since the secondary mineral is likely to have crystalline properties differing from those of the missing shell-substance, it may fail to restrict its growth absolutely to the cavity, and will then obscure some of the details of the fossil. Thus the petrifications (in Beekite chalcedony) of Mollusca in the Upper Greensand show peculiar orbicular surfaces that were certainly not present in the originals (Pl. iv. fig. 2). It is clear that the nature of the mineral deposited in the hollow depends on the quality of the aqueous solution available, and bears no relation to the original substance.

The great majority of vein-minerals may occur as pseudomorphs after organisms, but Silica, Calcite and Pyrites are those usually employed. Silica, typically as Chalcedony, often replaces calcite or aragonite in calcareous rocks containing opaline silica in the form of Radiolaria or Sponge-spicules. Such petrification is often most satisfactory, since the calcareous matrix can be removed with acid, the silica remaining un-

touched. In favourable cases details of form, both internal and external, can be exposed as clearly as if the fossil had never been encased by rock. Exquisite preparations of Brachiopod brachidia (Pl. xi. fig. 9) and Blastoid hydrospires can be made in this way; but alas! siliceous petrification of Invertebrates is rarely found in this country.

Calcite often replaces Aragonite in limestones, and may even form pseudomorphs after opaline sponge-spicules. Iron Pyrites, as Marcasite or Pyrite, is the usual petrifying mineral for argillaceous rocks. It is difficult in this case to determine whether the replacement has been subsequent to removal of the original, or by molecular replacement, since the opacity of the mineral hides any minute structure that may be preserved. Marcasite has serious disadvantages as a petrifying substance, since it is extremely unstable when exposed, and has a prismatic habit that may reveal itself in nodular outgrowths independent of the original cavity (Pl. v. fig. 2). Many Ammonites and other (usually Aragonite) shells from the Lias, Oxfordian and Gault are represented by Marcasite pseudomorphs that are obscure in themselves, and difficult to preserve after extraction. Pyrite, which is more characteristic of older argillaceous rocks, is quite stable, but its pronounced cubic crystallization may cause destruction of surface details. However, in some instances, it proves an admirable replacing mineral, since its hardness is usually greater than that of the matrix. The Devonian Starfish from Bundenbach, which can be cleared of their slaty covering with a brass-wire brush, show Pyrite in its most satisfactory rôle as a petrifying mineral.

In Sandstones, where the substance of the fossils is usually the only soluble material, petrifications may be

made of a great variety of minerals. Silica (often as Quartz) and Calcite still predominate, but metallic minerals may often form the replicas. Malachite, Blende, Hematite, Limonite and Galena may be cited as minerals occasionally found replacing fossils in sandstones (and even in limestones); while Barytes, Celestine and Selenite have been found as organic pseudomorphs in greywackes and clays.

(b) *By molecular replacement*

It is clear that the type of petrification above described can preserve no vestiges of the minute structure of the fossils replaced. Save for the peculiar character of the shape of the cavity available, the secondary mineral follows its own crystalline mode of accretion as faithfully in an organic cast as in a fissure or geode. But in some cases deposition of the replacing mineral takes place *pari passu* with removal of the original. Under such circumstances replacement is carried out with great perfection, so that the finished pseudomorph possesses every detail of microscopic structure of the fossil. Such accurate replacements are common among minerals (*e.g.* Quartz after Crocidolite) and in the silicification of woody tissue; and they are not unknown among Invertebrate fossils. Shells and tests from the Upper Chalk may sometimes show patchy petrification by silica, especially when associated with a flint-nodule, but the replacement is rarely complete.

(IV) DISTORTION AND DISFIGUREMENT (Pl. iii. fig. 3)

Perfect specimens of fossils, even of the commonest kinds, are relatively rare. To the numerous abnormalities, diseases and accidents that may mar an organism

during life, or cause its death, have to be added incalculable, but always serious, risks of *post-mortem* damage. The majority of shells are broken before they reach the sanctuary of a sedimentary grave. The scour of waves or insidious attacks of the weather, and the unsympathetic investigations of carrion-feeders, will pass over few of the organic remains exposed to them. Sedentary animals find congenial foundations on empty shells, while those of retiring habits welcome the soluble fabric for excavation of their crypts.

Fossils embedded in sandstones or limestones are liable to be crushed unless their cavities are filled with sediment or concretionary matter. Brachiopods and Irregular Echinoids are especially affected in this way, owing to the small size of their foramina and consequent imperfect infiltration of sand or ooze. But in general fossils in such matrices do not suffer mechanically after entombment. In argillaceous rocks, on the other hand, no hollow shell is safe (however well filled with clay) unless a concretion has developed within it. The pressure that converts clay to shale works equally on the materials inside and outside the fossils, so that the latter are inevitably flattened. The more severe stresses and strains that produce slaty cleavage will involve the fossil-contents in shearing; so that the already flattened shells take on lateral distortion. At some horizons in the *Lingula*-Flags, *Lingulella davisi* may be collected in great abundance, but hardly two specimens out of hundreds will have the same shape. Even when cleavage is incipient, fossils are distorted (see Pl. iii. fig. 3), while development of complete slatiness usually renders organic traces practically unrecognizable.

In slowly forming sediments, empty shells become encrusted by organisms of sessile habit. Frequently Hydrozoa, Polyzoa and Worms grow on the surfaces

of lining shells in symbiotic relationship with their owners, but after death similar animals may mask the superficial features, external and internal, and penetrate the substance; just as Barnacles encrust, and ship-worms perforate, a wooden hull. Quite long "lists of fossils" may sometimes be compiled by enumeration of the species of Hydrozoa, Madreporaria, Polyzoa, Brachiopoda, Serpulids and Pelecypoda adhering to Chalk Echinoids, while the test itself may be so smothered under these growths that even generic determination is doubtful.

(V) IMPRESSIONS AND TRACKS

The bodies of dead animals lying on soft silt, or those of living ones moving across it, leave impressions more or less corresponding with their shape and structure. Thus the surface of a modern beach is broken by worm-castings and tracks, burrows of Heart Urchins, Razor-shells and Sand-fleas, footprints of Crabs, and stranded forms of comatose Jelly-fish. In most cases these traces of abundant life are obliterated at the next tide; but since, like ripple-marks, they extend into shallow water below tidal limits, they may be covered by new layers of sand or clay without much disturbance if the weather is calm and deposition is in progress. Just as ripple-marks, and other inorganic irregularities, are commonly found in littoral deposits of all ages, so organic vestiges are often perpetuated. The perfection of such markings depends largely on the texture of the silt, while their interpretation is bound to be uncertain if their makers belonged to extinct groups. The sinuous grooves and coiled casts of "lug-worms," and the blurred tracks of Nereids, look much the same whether made in Lower Palaeozoic times or yesterday. The confused, but re-

solvable, impressions of collapsed jelly-fish or partly decayed Holothurians are none the less distinctive, whether the period of their production was Holocene, Jurassic or Cambrian. Although such traces rarely provide opportunity for appreciation of the anatomical qualities of the animals that made them, they at least prove the existence of various types (often incapable of direct fossilization) in remote periods. It is interesting to find that "worm-tracks" occur well down in the Pre-Cambrian of the Longmynd and elsewhere, in slates that contain no other recognizable fossils. These rough markings thus carry back indications of life (and that of a fairly high order) far beyond the limits at which ordinary palaeontological evidence fails. Fine Cambrian silt in British Columbia has yielded wonderfully clear impressions of Medusae and Holothurians, while the Upper Jurassic Lithographic stone of Solenhofen includes similar relics.

Closely akin to impressions of past organisms are the tubular aggregates of fish-scales found in the Chalk, and ascribed to the activities of marine Annelids. These protective tubes recall the familiar "caddis-cases" of modern rivers. They afford some evidence as to the fishes of the period, and suggest the existence of worms; but they are hardly satisfactory as fossils of either group of organisms.

CHAPTER III

TECHNIQUE

(A) COLLECTING

(I) PURPOSE IN VIEW

ALTHOUGH the imperfection of the palaeontological record is such that no fragment of fossil evidence should be lightly thrown aside, collection of every specimen seen is usually impossible. Few as the fossils are in comparison with the organisms they represent, they are often exceedingly abundant. To collect all accessible fossils in some deposits would involve removal and storage of whole strata. It is necessary, therefore, to pick and choose among the lavish display of organic remains sometimes spread before the collector. Unless his purpose is the idle one of picking up "pretty" and striking fossils for use as ornaments or curios (in which case his needs will not be considered here), the average fossil-hunter will have special interest in some aspect of Palaeontology, and will direct his collecting towards the solution of particular problems. If his aim is stratigraphical, he will secure specimens of types known to have reliable "dating" qualities; if it is palaeontological, he will eagerly collect fossils of his chosen group, passing by others that might appeal equally to a colleague. In either case, it is good for collectors to "hunt in packs." It is unlikely that an individual will see all the fossils

that are exposed on a quarry-face ; second examination almost always reveals specimens previously overlooked, especially if the search is made by another collector. Further, it may often happen that fossils discarded by the one are *desiderata* for the other.

Whatever may be the immediate object of search, a collector should always bear in mind the following principles. First, if the deposit is but sparsely fossiliferous, collection of *all* its organic contents, whole or fragmentary, is important. Secondly, perfect fossils, whether of the kind specially sought after or not, must never be left behind, unless their removal is a physical impossibility. It is mistaken and useless charity to leave good specimens to cheer the next comer. Long before he arrives they will probably have been ruined by weathering or buried in talus. Unlike rare plants or insects, fossils do not propagate their kind. Rather take them while they may be gathered, and find them an appropriate owner afterwards, keeping them safe the while. Thirdly, a fragment showing morphological structure is often worth twenty whole specimens in which details are obscure. Fourthly, a fossil that cannot be identified in the field should always be brought away. After preparation and careful study it may prove to be a worthless fragment of a common type (when its subsequent treatment is clear); but it is quite as likely to be something new, to the collector if not to Science. Lastly, if the purpose of collecting is stratigraphical, at least one example of each species recorded should be preserved. Faunal lists ought never to be made (especially for publication) without actual specimens retained for reference. Attempts at specific determination at the time of collecting are attended with too many difficulties to yield reliable results, while the most careful and experienced student may

make mistakes. These can be rectified if the specimens are available, but must always remain as sources of further error and confusion if the printed name has no solid backing.

(II) REGARD FOR STRATIGRAPHICAL POSITION

The precise horizon from which a fossil was collected is one of its most valuable qualities, whether it is destined for geological or biological treatment. This point can easily be determined at the time of collection (unless the specimen lay on a spoil heap, when due note of the fact should be taken, and attempts made on the spot to trace its actual provenance), but it cannot be subsequently deduced with certainty. Before undertaking an expedition, it is well to study available accounts of the district and strata to be visited, so that determined stratigraphical divisions can be recognized. But in any case, the first duty for a Palaeontologist, on his arrival at an exposure, is to note, and if possible to measure, the more striking features of lithology and bedding shown in the rocks. Not until this is done should any collecting begin. Since the fossil-evidence may often supply other, and better, indications of zonal horizons than mineral qualities, the first sketch of the exposed rocks may need revision. It is usually best to fix on some prominent and persistent feature (such as a shale-band in limestone, a calcareous layer in shale, or a flint-bed in chalk) as a datum from which vertical measurements can be made; the distance above or below such a line at which any fossil or fossil-band occurs should, where possible, be recorded. It is not enough to gather all the fossils from one quarry into a separate group, nor even to distinguish between those from upper and lower parts of the section. Too much precision in this matter is

impossible; too little will sooner or later lead to vain regrets. Stratigraphical divisions that seem adequate at one time may prove far too vague in the light of further research—zonal stages undreamed of by one generation become the dominant features of stratigraphy for the next.

It must be admitted that meticulous care in fixing the horizons from which fossils have come is tedious, and demands patience and stern self-control on the part of a collector eager to "try his luck." But without such precision, fossil-collecting ceases to have a truly scientific value, degenerating into an idle, almost vicious, hobby. No amount of subsequent repentance can re-endow a fossil with the value that has been thrown away by careless or casual collecting.

(III) LARGE AND MINUTE FOSSILS

In general the tools required by a field-palaeontologist are essentially similar to those necessary for any geological work. A light pickaxe, hammers, a cold-chisel, a pair of pliers, a bricklayers' trowel, and ample supplies of small boxes and old newspapers constitute the apparatus most often useful. It is always satisfactory to have at least two hammers (both with square heads and chisel edges), one weighing about a pound for quarrying or hitting the chisel, and one quite small for trimming specimens. It is, of course, needless to take all types of apparatus on most expeditions; the selection will be determined by the nature of the rocks likely to be encountered. Hammers and chisels are of little use on soft clay (though the former should always be taken in view of possible nodules), while a trowel is ineffective on hard rocks.

When the objects of search are macroscopic fossils,

first attention should be paid to weathered rock-surfaces that are usually to be found on natural or artificial sections. Not until this examination is complete is actual quarrying advisable. In most cases, if fossils do not appear on decaying surfaces, they are less likely to be seen in newly fractured matrix. If a portion of a fossil is seen protruding from hard rock, its surroundings should be carefully studied with a view to finding cracks or other lines of weakness along which fractures can be made. In all cases where hammering is required, care should be taken to let the blows fall as far from the specimen as is consistent with its ultimate extraction. Never attempt to break out the fossil, but aim to collect the piece of rock in which it is embedded. When possible, it is a valuable safeguard to keep one hand over the specimen while using the hammer, since it may fly off unexpectedly and be lost to sight.

It is often easier to pick up fossils from the talus or quarry-heaps than to dig them out from a rock-face, and still less exhausting to purchase them from the quarrymen. Such aids to collecting should not be ignored; but it is essential to remember that specimens thus acquired have not the same certainty of stratigraphical horizon. However, it is often possible to trace the bed from which such fossils have come, usually by comparison of their matrix with that of the main section.

If minute fossils are required (*e.g.* Foraminifera, Ostracoda, or small shells), collection of individual specimens is clearly infeasible. Any friable or rotted layer may contain such organisms, and it is best to transfer the loose material to tins in bulk, taking the risk as to whether later examination will prove it prolific or barren. In some cases it is possible to gain some indication of the quality of such material before

adding it to the day's load. A small quantity may be put into a gauze bag (say, a small butterfly-net) or a fine sieve. If the rubble is dry, a short spell of vibration will drive the finest powder through the mesh, and the gritty residue can be inspected with a hand-lens. If it is wet, the same result may be obtained by vigorously shaking the container under water. It is usually possible to detect small fossils in the residue, and to form an estimate of their relative abundance. But failure to find them by this rough method is no proof of their total absence; it should merely influence the collector in determining the bulk of material worth carrying. Students of Microzoa are well advised to bring away samples of all sedimentary rocks exposed in each section. Many compact masses may be resolved into powder by suitable means, while the others can be sliced for microscopic examination. Experience will soon show the types of matrix most likely to yield small fossils.

(IV) FIELD PREPARATION

The limitations of human strength demand that the items of a day's "bag" shall have the smallest size compatible with their safety. Hence, when a fossil is firmly embedded in matrix, it is expedient to reduce the bulk of the block. But it is never safe to aim at complete extraction of the fossil at this stage. Not only does adherent matrix act as a protection to the specimen during carriage, but it often affords useful proof of the layer from which it was collected. When possible, use of a hammer in the rough trimming of specimens should be avoided. The vibration caused by blows often shatters the fossil, even though care is taken to strike distant parts of the block; while the uncertainty of the direction of fracture involves risks

that should not be lightly taken. A pair of blunt pliers are the safest means for reducing the matrix, although they are only effective on thin edges. If hammering is necessary, it should be applied lightly. A small hammer, with which a rapid succession of taps is given, proves less dangerous than a heavy one. The block should, when possible, be held in the hand during trimming, so that vibrations may be absorbed. If it is too large to hold, a tuft of grass or moss gives a safer foundation than hard rock. Never try to chip off large pieces at a time.

If a crack appears in the fossil, in spite of precautions, three courses are available. Unless the block is still too large to carry, stop. It may be possible to continue its reduction safely at home or in the laboratory. If the mass is large, it is best to give a sharp blow that splits the specimen in half. Each segment can then be trimmed separately (care being taken to avoid alteration of the accidental fracture), and glue will subsequently minimize the effects of the disaster. Thirdly, throw away the specimen and look for another. This confession of failure should be made only if the specimen has crumbled, or if there are plenty more of the same kind in the same layer. So long as a fossil is recognizable, it retains some value even in ruin.

(V) FIELD LABELLING AND PACKING

It cannot be too strongly urged that a fossil-collector, in common with other scientific workers, should proceed at every stage as though the sword of Damocles were suspended above him. This does not imply that there is anything intrinsically dangerous or fatal in the work. But even though bodily dissolution may be far distant, mental failure is an ever-present danger. Never trust

to memory. Impressions gained while collecting are vivid enough at the time, but they rarely last until the "finds" have been sorted and labelled at home. If a succession of exposures is visited in one day, details of the various experiences become confused. Further, even though memory may suffice to recall each episode for a short time, the uncertainty of human affairs may demand a long interval between collection and examination of material. The day's bag may not be unpacked for several weeks, and the hand that unloads it may not be the one that filled it. Unless the details noted during the expedition are enclosed with the specimens *in writing*, much essential information will be permanently lost. It is not enough to enter details in a notebook, although such records should always be made. A label must be enclosed with, and indeed fastened to, each specimen before the quarry is left. A supply of stamp-edging, or other gummed paper, does not add materially to the weight of apparatus carried; but it may prove the most valuable item thereof.

The label for each fossil should record two facts: first, the precise horizon, with reference to a fixed and *permanent* feature of the exposure; and second, the locality. The latter should be indicated in such a way that anyone, with the help of a map, could locate the section, whether on the spot or in the study. Labels are best written in ink or indelible pencil; time, or a drenching shower, may obliterate words written in blacklead.

For purposes of transport, every specimen must be wrapped in paper or similar material. If several fossils are enclosed in one sheet, care must be taken that at least one thickness of paper separates each from its neighbour. Without this precaution, some or all of

the specimens will be ruined by attrition. Small fossils are best packed in boxes or tins, surplus space being filled with moss or grass. Even so they must be wrapped in paper, lest green stains soak into and disfigure them. An excellent plan for safe removal of friable shells extracted from clay is to gently bury them in some of their own matrix enclosed in a tin. They will be secure against ordinary vibration, and can be washed out quite safely if unpacking is not unduly delayed.

(B) PREPARATION

(I) NEED FOR PATIENCE

Extraction of fossils from matrix, and further processes preparatory to study, may be compared with dissection of biological material. In both cases practice affords the only means of acquiring skill, and early attempts must often lead to the sacrifice of cherished specimens. It is erroneous to imagine that cleaning fossils is a rough-and-ready business; the delicacy of touch and deliberation required are in no way inferior to those necessary for anatomical work. Indeed, in some respects the greater restraint is imposed upon the Palaeontologist. An anatomist usually has reliable knowledge of the resistance that tissues will offer to his scalpel; but no constancy of texture can be assumed for a matrix. Frequent need for application of considerable force demands constant watchfulness, lest the tool should slip into soft material and reach the specimen.

One advantage over the Zoologist lies in the durability of palaeontological material. There is no need to hasten dissection lest the object should decay; in many cases the refractory nature of matrix is mollified by

delay. Specimens "developed" to the utmost limit of safety often permit removal of further particles of rock when examined after months of storage. In any case there should be no trace of haste in the preparation of fossils. It is very tedious to spend hours in removal of matter whose absence makes little apparent difference; and, in view of the frailties of human nature, it is unsafe to spend too long at one sitting on any specimen. Sooner or later the "finicking" efforts with brush and needle create an overwhelming desire to attempt more heroic methods. Resistance to temptation is made hard by the knowledge that a violent blow *might* produce the desired result not only more quickly, but more effectively, than piecemeal picking. Moreover, recollections of success following previous falls from grace convert this possibility into probability at that stage of exhaustion. But the author, with grievous reminiscence of avoidable tragedies, recommends that whenever such feelings arise the worker should put away, not the temptation only, but the specimen. The surest cure for all troubles, whether of mind or matrix, is a night's sleep. For nerves and muscles thus refreshed, another spell of labour will have lost much of its dreary monotony. Knock out in haste, and repent at leisure, is as true in this connexion as the more familiar form of words in another; exceptions may occur in both cases.

(II) SEPARATION OF FOSSILS FROM MATRIX

Brief suggestions as to familiar and effective methods for the cleaning of fossils follow, but there is no intention to propound any fixed rules. Every specimen presents its own problems; while most experienced workers devise and perfect means of preparation suited to their own ingenuity and requirements. Fairly detailed

accounts of many processes are published in "guides" of the British Museum and Smithsonian Institution, and in a paper by Dr. F. A. Bather in vol. viii. of the *Museums Journal* (1908). In a general introduction to the technique of fossil-preparation, it is more appropriate to convey a series of hints than to describe elaborate schemes rarely adequate for the full solution of particular problems.

The removal of matrix, and the methods employed therefor, will depend chiefly on two conditions. Matrices differ in texture from soft clay to concretionary matter with the hardness of steel; while variation in the durability of fossils is hardly less wide. In the relation between these two qualities lies the problem before the worker, whose aim is to destroy the one, and preserve, or even reinforce, the other. Fossils are usually either harder or softer than their containing matrix. Those in soft rocks are usually friable, but the converse is not always true.

If the fossil is harder than the matrix (whether by original character or petrification), and is tolerably coherent, a brush is the safest kind of tool. For calcite shells in loose limestone or clay, no more elaborate apparatus than an old tooth-brush is required. These may be procured in varying degrees of stiffness, or can be graded by cutting the bristles. Rotary brushes may be used in a dental engine, but hand-work is less likely to carry the process too far. In matrices of the nature of chalk, brushing is best carried out in the dry; though care should be taken to avoid inhaling the dust, which may cause a kind of "hay-fever." In clays, if the fossils are coherent, the brush may be moistened, but the specimen should never be saturated. It can be occasionally cleared of mud by rinsing for a few seconds under a gentle stream. Fossils too small to be handled

individually can be sorted, and often sufficiently cleaned, by placing them at the top of a pile of sieves (becoming finer downwards), and directing a steady jet of water through the whole.

It often happens that shells in clay are so friable that they cannot withstand brushing, however gentle. In such cases, both fossil and matrix must be reinforced with glue or shellac. The whole specimen should be soaked in dilute solutions of one or the other reagent, and allowed to set hard. The matrix can then be painted locally with water or alcohol, and gradually brushed away.

When the matrix is too hard to yield to a brush, it may either be softened chemically or chipped off mechanically. Both methods are fraught with danger, since in many cases rock and fossils are of similar chemical composition, while even petrifying substances are rarely harder than steel.

In the case of fossils preserved in partly amorphous limestone, "weathering" can be imitated by leaving the lump for some weeks in water through which carbon dioxide is slowly bubbled. This is preferable to exposure to rain-water, since the latter often leads to the growth of green stains, while its intermittent application encourages precipitation of hard calcareous crusts. Occasional bouts of brushing will slightly accelerate this tedious process. Soaking in strong sugar-solution has a similar effect, especially if the liquid is hot; but great care is necessary to remove all traces of sugar before drying, lest its crystallization should crumble the surface of the fossil. Hydrochloric acid (or, preferably, acetic acid) may be painted on to the matrix remote from the fossil; but, unless the latter is a siliceous petrification, it must never come in contact with the shell. In the case of calcareous fossils in a

non-calcareous matrix, strong caustic potash may be used, but it is not invariably effective, and needs complete removal before the specimen is dried.

Mechanical means for removal of matrix are more generally applied than chemical ones, and give more scope for individual skill. It is a good plan to leave a small portion of rock on the specimen, if this is possible without hiding some essential structure. The matrix not only affords a clue to the horizon from which the fossil came (invaluable in event of loss or displacement of the label) but may serve to suggest the conditions under which the organism lived. In attacking the matrix near the fossil, pressure is better than blows. The direction of pressure should always be perpendicular to the shell-surface. Never scrape or scratch the material; try to ease it off in chips or grains. If the rock gives way suddenly, and the tool touches the specimen, only a prick will result if these precautions are taken; otherwise a slash or groove will disfigure it. Similarly a pointed tool is better than a knife. The most efficient implement is a thick needle (set in a handle), ground to an angular, blunt pyramid at the tip. In many cases it is helpful to keep the specimen under water, and to watch the removal of each grain under a binocular dissecting microscope.

(III) DISSECTION OF FOSSILS

With the exception of Echinoderm tests, Invertebrate hard-parts are normally external structures. They often exhibit superficial excrescences and other ornament that have but slight relation to actual anatomy, useful though they may be for specific identification. The anomalous position is often reached where the species to which a fossil belongs can be readily determined, while its generic

or even family status is not apparent. The principles whereby such groups as Corals, Brachiopods and Pelecypods are classified are based largely upon features invisible on external examination. It thus becomes necessary to excavate the included matrix, with more or less inevitable destruction of the surface of the fossil examined. Fortunately, imperfect specimens are more abundant than complete ones, so that the wastage consequent on dissection can usually be limited to examples unsuited to fill honoured places in a collection.

The mode of dissection adopted will be determined partly by the condition of the matrix, and partly by the nature of the organism. There are three methods generally available for exposure of internal structures in fossils. If the infilling is loose, a portion of the shell may be filed away, and the interior cleared by means similar to those used for the outer surface. If the contained matter is hard (a frequent condition, especially in cases where concretions develop), the shell may be entirely removed, leaving a mould which shows internal features in negative. If neither of these methods is satisfactory, resort may be had to sectioning fossil and matrix together.

For the study of Corals and similar forms, the last-named process is necessary. Transverse and longitudinal sections can be obtained by grinding specimens to the required level, and either polishing the surface or preparing a thin slice for transparency. By cutting the specimen transversely, a series of sections can be taken across a single corallite at different levels, to display developmental stages. In many cases, where a fossil is too delicate for extraction, or encased in very refractory matrix, serial sections comparable with those made by a microtome can be prepared. The sections cannot be preserved like those in a "ribbon" of paraffin wax; each is

destroyed in making the next in sequence. The specimen should be rigidly fastened to a flat plate, and ground away until signs of the required structures appear. The surface should then be cleaned (preferably by a wash of dilute acid), and photographed or carefully drawn. Grinding may then be resumed until a measured thickness has been removed, and the delineation repeated. If the amount destroyed at each episode is recorded, and the representations of each surface are to the same scale, models in wax or card can be constructed. Special apparatus has been devised for this process, but it can be carried out with fair accuracy by hand after some practice. The method is well adapted for study of Brachiopod or Pelecypod hinges, although it has been employed most frequently on Vertebrate skulls.

A simple and valuable modification of grinding was perfected by the Rev. Norman Glass for display of Brachiopod brachidia; the results of his process can be appreciated in the illustrations to Davidson's monograph. The tightly closed valves of Brachiopoda often failed to admit fragmental debris, so that their cavity became filled with crystalline calcite introduced in solution. The softness and transparency of this infilling, deposited so gently that no internal structures are damaged, makes possible display of brachidia by scraping away the shell and surplus calcite, polishing the residue (when the opaque shell-ribbons are reached) by dilute acid.

Natural moulds of Conchifera often retain impressions of muscle-scars and pallial lines. When such material is not available, artificial moulds may be prepared, provided the infilling material is compact. The most efficient method is that of "burning." In some cases, especially when the matrix is only partly calcareous, the shells can be actually calcined and removed by brushing. In others,

the specimen may be heated (insufficiently to induce chemical change) and suddenly plunged into cold water. The laminate fabric of the shell tends to flake off, and careful repetition of the process will expose a clean mould. Recent application of this method to Jurassic Brachiopoda has almost revolutionized the classification of some groups.

(IV) STAINING

In those fossils that have sutural lines or fine ornament and pores, it is often difficult to detect details owing to the similarity in colour between shell and matrix. This applies particularly to fossils from the Chalk. In those, the porosity of the rock and relative compactness of the fossil invite application of a soluble stain. This is absorbed by the chalk, and may be washed off from the calcite. By such means, ambulacral pores or Polyzoan zooecia are clearly brought out. The tracing of sutures is important in the study of Echinodermata, Cephalopoda and Trilobita. In Crinoids and Echinoids, divisions between the plates can be detected, or made more apparent, by suitable treatment. On well-preserved surfaces, suture-lines occur as very fine grooves. These can be intensified by application of a stain giving a granular precipitate. One of the best reagents is Indian Ink freshly diluted with water. A few moments after the fluid has been painted on to the moistened surface, before it has begun to dry, the whole specimen should be lightly rubbed with the finger or a cloth. The stain on smooth parts is removed, while that in depressions is left. A brush must not be used, since the bristles scour out the grooves and give disconcerting results. An excellent method for displaying suture-lines on pyritous moulds of Ammonites consists in soaking the specimen in dilute size, and rubbing chalk, or prefer-

ably a heavier white powder, over the surface. The powder works its way into the narrow septal spaces, while continued rubbing prevents its adhesion to the chamber-walls.

(V) STORAGE AND PRESERVATION

Whether a collection of fossils is displayed in cases or cabinets, or stored in boxes for occasional reference, the one thing needful for its safety is cotton-wool. The utmost care should be taken to keep specimens from touching one another. The practice of fastening fossils with glue to wood or card is to be deprecated. Specimens thus stuck down cannot be properly handled for study, while attempts to release them often lead to disaster. Minute fossils, which may get lost in wool, can be stored in glass tubes, in the bottoms of which felt has been fastened.

Most fossils, if protected from shock or attrition, may be trusted to remain intact for indefinite periods. But some, especially petrifications in marcasite, soon disintegrate unless precautions are taken. The preservation of pyritous fossils is one of the most difficult problems associated with practical palaeontology. When exposed to moisture, Marcasite rapidly decays into Sulphurous acid and Ferrous sulphate; disintegration is often indicated by efflorescence of the latter. The change depends on the presence of damp air, so that inclusion of a little Calcium chloride or washing soda with the specimen will retard decay, though it cannot prevent it entirely. Small specimens can be preserved in petrol or similar oils, but this is usually inconvenient. Marcasite fossils can only be maintained in good condition by frequent examination. At the first sign of decay the specimen should be soaked in a solution of caustic

potash. After immersion for a few hours, the alkali can be neutralized with hydrochloric acid, which must be removed in turn by washing in distilled water. In some cases access of air can be prevented by coating specimens with wax or varnish.

Friable shells are best preserved by impregnation with size or shellac. The latter (in alcoholic solution) is preferable, since it does not become sticky in damp surroundings. A trace of corrosive sublimate added to either solution inhibits the growth of mould, which may otherwise cause trouble.

The methods of mounting microscopic objects such as Foraminifera or Radiolaria are similar whether the specimens are recent or fossil; no details need be given here. It may, however, be noted that such small fossils (when separated from their matrix) are usually best studied in reflected light, and can be placed in air cells rather than any special medium.

(C) TAXONOMY

The classification and nomenclature of fossils is attended with difficulties far greater than those encountered in biological taxonomy, serious as they may prove when living creatures are concerned. Increase of knowledge leads inevitably towards complication of classification, since all schemes involve more or less arbitrary subdivision of series that are essentially continuous. No two organisms are likely to be exact duplicates, even when they belong to the same generation or are born of the same parents. So that in palaeontological material, where a difference in horizon of a few feet may mean the separation of two related organisms by many series of generations, accurate definition of specific characters is inconceivable. No

fewer difficulties appear when classification is attempted on a broader basis. The restriction of evidence to durable structures, whose modifications often have little connexion with those of more "vital" organs, cannot but impair the quality of systematic grouping. Moreover, it compels adoption of different principles from those employed in Biology. Sections of the Echinoidea based on characters of pedicellariae, of Gastropoda on the distribution of radular teeth, or of Cephalopoda on the number of branchiae, can never be recognized by Palaeontologists by direct observation, although they may be far more sound than the makeshift schemes that have to be erected. When recent representatives of fossil groups exist, it is often possible to apply zoological classification provisionally, but the inclusion of many forms in "malacological" divisions must always be tentative. The normal trend of zoological research seems to lead its devotees to overlook the shells or skeletons of Invertebrates in their eagerness to study the soft tissues. This regrettable tendency is less marked in the case of Vertebrates, but for many Invertebrate groups analysis of the hard-parts of living forms has been left to Palaeontologists, who sought in vain for the information they needed in the records of biological literature.

There is a constant temptation, by no means restricted to Palaeontologists, to regard the application of a name to every specimen as a sufficient end, after whose attainment the fossil is "done with" except for storage or display. Necessary though names must be, they are not attributes of the organisms, but merely conventional terms designed to facilitate reference. A fossil continues to display its morphological peculiarities whether named rightly, wrongly, or not at all; appreciation of its natural qualities, absolute and relative, is far more

important than anxiety over its place in artificial taxonomy. Further, if the former investigation is adequate, the latter detail should automatically follow. Ideally, and it may be hoped usually, names are given to forms as indications of their possession of certain observed qualities distinguishing them from, or affiliating them to, other forms; additional specimens can be identified with those previously described only after morphological study comparable with that made by the authors who gave the names. At least, it is essential to make sure of the precise significance attached to names before rashly applying them to new material.

Whenever possible, reference should be made to the paper in which a name was originally proposed. Better still, the specimen or specimens which caused the introduction of the name should be examined, and compared with the example whose identification is sought. Failing either of these important aids to accuracy, use may be made of later monographs in which the genera and species were redescribed by authorities. If the latter guidance is necessary, due note should be made of the fact, since cases are by no means lacking where specialists have attached names to forms different from those to which they rightly pertain. Especially in the publication of lists of fossils for stratigraphical use, care should be taken to give references to the descriptions and figures used in making the identifications. The usual, and proper, course of placing immediately after a specific term the name of its original proposer, may prove misleading unless his actual specimens or descriptions have been studied. An example of this danger is afforded by one of the best-known "characteristic fossils" of the Lower Oolites. In 1829 Phillips proposed the name *Clypeus semisulcatus* for an Echinoid found in the Coralline Oolite of Malton; the species was later made

the genotype of *Pygaster* by Agassiz. By a series of errors and misconceptions, the specific name came to be applied to an allied, but quite distinct, form common in the Inferior Oolite of Gloucestershire. From 1857 onwards this Lower Oolitic Echinoid was always called *Pygaster semisulcatus*, the misapplication of the specific term being stereotyped in Wright's monograph. Later writers habitually referred to *Pygaster semisulcatus* ("Phillips") when dealing with the Inferior Oolite form, when, as subsequent research has proved, the species meant was "*P. semisulcatus*, Wright (*non* Phillips)." Had their references been made in the latter way, much confusion would have been prevented, since *P. semisulcatus* (Phillips, *non* Wright) is an entirely different species, and occurs in the Corallian only.

Since confident identification of species demands long study, and often special knowledge of the groups concerned, it is practically impossible for a stratigrapher to definitely and correctly name many of the varied forms that he collects. Unless the help of "specialists" in the different groups can be obtained, it is safer, and less misleading, to compare fossils with described types rather than to identify them. Especially since true identity between any two specimens is well-nigh inconceivable, a list of fossils which includes absolute specific determinations is less convincing than one in which the fossils are said to be *comparable* with species previously diagnosed. Greater experience, and more material, always tend to lessen the confidence with which specific names are applied; it is not furthering the cause of Science if Stratigraphers rush in where Palaeontologists fear to tread!

The foregoing comments apply to original work; their rigid adoption would make pedagogic palaeon-

tology impossible. The conception of species held by a specialist must differ from that held by an elementary student. For the latter, specific terminology must have greater latitude, so that forms similar in all fundamental characters will be grouped under a single name. Even so, systematic difficulties are bound to arise. One fertile source of confusion has been indicated above. Generations of students have been taught that *Pygaster semisulcatus* is a characteristic fossil of the Inferior Oolite, while *P. umbrella* is restricted to the Corallian. But it is now established that the name *semisulcatus* belongs by right of priority to the Corallian species, that from the Inferior Oolite having the specific name *ornatus*, while *P. umbrella* is a name with no precise significance. The same fate has befallen other well-known Echinoid names, such as *Ananchytes ovatus* (now called *Echinocorys vulgaris*) and *Galerites albugerius*, which, after a temporary sojourn in *Echinoconus*, has returned to *Conulus*. These irritating changes of nomenclature are not gratuitous pitfalls dug in the students' path, but represent attempts to apply to fossil species and genera the names given them at their first post-Linnaean description. It is unfortunate, but inevitable, that the types most often affected by systematic vagaries are the common ones, whose nomenclature became confused by frequent references before taxonomic rules were established. It is permissible to hope for eventual finality in such corrections and necessary to put up with inconvenience during the transition from chaos to order.

The second cause of complication is independent of actual error, resulting rather from progress in knowledge and refinement of classification. A few decades ago the "genus" *Ammonites* sufficed to include the myriad species now placed in scores of genera

and many families. Similarly the name *Rhynchonella* is restricted to a few peculiar species; the original "genus" included almost all the members of the family Rhynchonellidae of modern classification. The structural characters whose discovery has led to dismemberment of such comprehensive "genera" are often of real importance, but no less frequently difficult to appreciate without detailed study. A student of Palaeontology for its own sake can, and should, recognize recent generic divisions, and try to check their validity; but a student of Geology, whose purpose in dealing with fossils is to discover indices of stratigraphical horizons, cannot hope to prove for himself that any generic differences separate such well-known forms as *Terebratula sphaeroidalis* and *T. simplex*. It is, of course, possible for him to remember, parrot-wise, that the one is a *Sphaeroidothyris* while the other is a *Pseudoglossothyris*, but information gained at second-hand is not knowledge, and, in such a case, is of very doubtful value. For all but specialists, most of the Terebratulidae must be classed under the name *Terebratula* (*sens. lat.*); all Ammonites must be *Ammonites* still, though no single species can rightly claim such a generic prefix.

CHAPTER IV

GEOLOGICAL PALAEONTOLOGY

(A) STRATIGRAPHICAL

(I) ZONES AND HEMERAE

THROUGHOUT the last hundred years, Geologists have found in fossils efficient and reliable evidence for the chronological classification of sedimentary rocks. The claim made by William Smith, that "Strata [can be] identified by organized fossils," has been substantiated in the main; and the principle has been applied to refinements undreamed of by that pioneer. Subdivision of the geological record into the great eras Palaeozoic, Mesozoic and Cainozoic is based on palaeontological evidence, as the names imply; relatively brief periods of time, such as hemerae, are recognized solely by detailed study of fossils.

The classification of rock-systems was a fairly simple problem for early stratigraphers, who, starting from preconceived ideas, believed in the catastrophic doctrine that the faunas of successive periods were distinct, in members and origin. Long years of palaeontological research were necessary to prove that the "dating" evidence afforded by fossils is not so sharply defined, while growth of realization of the process of evolution was fostered by, and contributed to, the knowledge that each faunal assemblage is intimately connected with its antecedents and successors. When species ceased

to be regarded as immutable, sharp divisions between stratigraphical stages disappeared. Biological and geological systems of classification came to be moulded into different, and more plastic, forms, whose lack of the old-time precision proved inconvenient, but natural. It is, perhaps, fortunate that subdivision of geological time into its main sections was carried out by believers in catastrophes and special creations, since it supplies a necessary basis for arbitrary classification, and would be difficult to establish with the further knowledge now available. Just as the genera and species diagnosed by Linnaeus and his followers are still recognized, though the conception of their value has altered; so the geological periods named by Smith, Murchison, Sedgwick and Lyell serve as convenient excerpts from eternity. It is a striking testimony to the accuracy and insight of the founders of Stratigraphy that their schemes of classification, based on limited experience and philosophical misconception, can still be maintained, with but trifling modification, after a century of discoveries made possible by their efforts.

The student of Historical Geology has to reckon with two factors, stratigraphical and chronological respectively. It is necessary to bear in mind that the amount of work done is dependent on, but in no sense commensurate with, the time spent upon it. Thus one and the same interval of time may be represented by the accumulation of a thousand feet of sediment in one place, ten feet in another, and the removal of material by denudation in a third. While stratigraphy (literally interpreted) can record and correlate events that have happened in course of time, it can supply no reliable evidence of the duration of time itself. Physiological conditions (on which deposition of strata depends) are too variable, in time and space, to give

an equable and unbroken record. On the other hand, organic evolution proceeds with relative uniformity. Acceleration and retardation, progress and reversion, tend to qualify that statement in detail, but do not affect its general truth. Just as wider stratigraphical knowledge has bridged many of the gulfs that used to be attributed to cosmic catastrophes, so further discoveries among fossils have linked together many groups previously regarded as widely separate. While "saltations," or, for that matter, supernatural "special creations," cannot be considered disproved, occasions where such phenomena can be invoked grow steadily fewer as research continues; apparent breaks in the sequence of evolution are more probably due to ignorance than to reality. It may be doubted whether the actual rate of evolution, if such exists as a definite principle, will ever be determined with sufficient precision to allow of actual "dating" of geological time; but the direction of its progress, in the main current and tributary streams, is demonstrable enough to indicate relative chronology.

Since a geological period is the sum of its component hemerae, clear realization of the significance of the part will engender accuracy in definition of the whole. The term "hemera" represents an essentially biological conception, but has stratigraphical applications. In the course of evolution of species, each lineage is believed to attain a more or less prominent "acme," when its morphological qualities are relatively static, its distribution commonly wide, and its numerical strength marked. The components of a fauna do not attain their acmes synchronously, but the several lineages rise and fall, some rapidly and some slowly, with some measure of independence. Selection may be made of forms which show great acmaic prominence, and reach

their highest development successively. The time during which such a lineage maintains its acmaic qualities, biological and numerical, is called the "hemera" of that series. In strict terminology, any deposits that may accumulate during the hemera are the "zone" characterized by the group of organisms. If this distinction is borne in mind, it becomes manifest that zones may, or may not, be represented in various places, their existence depending on opportunities for rock-deposition during their hemerae. A hemera is a section of time (as the name suggests); while a zone is the tangible result of local episodes transacted in the specified interval. Thus, while it is perfectly justifiable to record that a zone does not occur in a certain locality, it would be absurd to suggest that a hemera was absent, although it may be unrepresented by actual materials.

The least satisfactory character of hemerae is their determination through evidence supplied by particular fossils. Although most species prove to have wide ranges at their times of acme, they rarely become world-wide—the most cosmopolitan forms are usually those of long duration whose extended acmes show little prominence. But a race of organisms whose vigour is such that its members would be chosen as hemeral indices will normally have representatives in all parts of the world where conditions are suitable; and the marked tendency to synchronous parallelism in the evolution of homogenetic stocks will usually produce "complementary" species that replace the missing guides and fulfil their rôle. In consequence, it is often most satisfactory to consider a hemera to be indicated by a morphogenetic "mode," or phase of specialization, than by any special specific types.

A zone may be recognized by the presence of the hemeral index in an acmaic stage of evolution, but is

more satisfactorily determined by consideration of its entire fauna. The index-fossil may have been of such a nature that it could not exist, or at least flourish, under certain physiographical conditions, but it is probable that some of its associates were more catholic. It not infrequently happens that two or more organisms, belonging to entirely different groups, reach acmaic stages at about the same time. Thus in the Upper Chalk, the Belemnite *Actinocamax quadratus* and the Echinoid *Offaster pilula* both characterize the same zone, which is named after the former type. But while the distribution of the Belemnite is somewhat sporadic, that of the Echinoid is more uniform, so that the *quadratus*-zone can often be recognized without discovery of a single specimen of the "name-fossil."

Since recognition of hemerae dates back no further than the early years of this century, while zones were proposed fifty years before, it is natural that the conception of a zone as the material deposited during a hemera is a modern refinement. Hence many "zones" that still do good stratigraphical service have no real chronological precision, but are of the nature of "sub-periods." Like larger divisions of sedimentary rocks, they are identified by the specific and proportional qualities of their fossil-contents. While such zones can be easily recognized in their middle portions, they tend to have ill-defined boundaries; in many cases they prove, on further palaeontological study, to spread over several hemerae.

It may be anticipated that the stratigraphical classification of the future will be graded in accordance with the acmaic stages of species or species-groups (hemerae), genera (stages), families (periods) and larger groups (eras). In a rough way, this grouping is already in use. The Lower Palaeozoic (or Proterozoic) era is

marked by the presence of Graptolites, Trilobites, and certain orders and suborders of Brachiopods that are either restricted within, or rare beyond, its limits. Similarly the Upper Palaeozoic (Deuterozoic) contains remains of plants, Fishes, Molluscs and groups of Brachiopods that are ordinarily distinct from those common in the preceding or succeeding eras. The Mesozoic is often called the "age of Reptiles," but some orders of Echinoids, Brachiopods and Molluscs (especially Cephalopods) are equally characteristic. The Cainozoic is the "age of Mammals." However, neither these great divisions, nor minor ones, can be defined with accuracy until Palaeontology has indicated the limits of hemerae, the units of geological time.

(II) CHARACTERISTIC FOSSILS

Acquaintance with fossils characteristic of the various periods is usually required of students of Geology, and is essential for those proposing to investigate stratigraphy in the field. The former sufferers deserve considerable sympathy, since the exigencies of examination courses rarely leave time for adequate inquiry into the biological characters of the fossils whose appearance, names and range they are expected to learn; while both classes of workers are often troubled by the varied opinions of authorities as to the particular species that are "characteristic." Moreover, Nature often adds to the confusion by local or sporadic distribution of common forms. It is usual, and correct, to describe *Hemicidaris intermedia* as a characteristic fossil of the Corallian; but while a worker in Wiltshire might perhaps collect specimens of that species by the bag-full, another in Berkshire, searching at the same horizon and in lithologically similar beds, would never find a trace.

Similarly *Conchidium knighti* is not merely "characteristic" of the Ludlow Limestone, but often constitutes much of its bulk; at Weo Edge, in Shropshire, single specimens can hardly be collected owing to the congestion of shells, but at West Knowle, about a mile away, the same bed of Limestone has not yielded a single example.

Such familiar species as those mentioned above have the merit of abundance in some localities (as well as that of restricted vertical range), but the same cannot be said of many types whose names figure in some lists of characteristic fossils. It is a fairly safe assumption that, granted sufficient knowledge and minute study, any fossil can supply precise stratigraphical evidence, whether it is common or scarce. To a casual investigator, the three abundant Echinoids of the Upper Chalk, *Micraster*, *Echinocorys* and *Conulus*, seem to persist with very little change throughout that stage. But to one well-acquainted with Cretaceous stratigraphy or Echinoid morphogeny, differences appear in specimens collected from horizons only a few feet apart. It is unlikely that the zonal progress recognized, and used, in these forms is peculiar to any special group of organisms. Nevertheless, appreciation of morphological refinements is impracticable for average geological students, so that discrimination of well-marked species and genera becomes necessary.

The author is strongly of the opinion that recognition of species should be left for students of Palaeontology, or those who carry stratigraphical studies beyond a preliminary stage. The chronological distribution of families and genera will give ample precision for elementary needs. Unless detailed work is in prospect, it is sufficient to know that Graptolites are characteristic of the Lower Palaeozoic—the dendroid types of the Upper

Cambrian, the less-branched Tetragraptids and Didymograptids of the Lower and Middle Ordovician, the Diplograptids of the Middle and Upper Ordovician, and the Rastritids and Monograptids of the Silurian. A mere list of the Graptolite species selected as zonal indices is sufficiently formidable; but when attempts to recognize and distinguish specimens, or even drawings, of the various species are made by students untrained in methods of palaeontological research, the foundations of belief are shaken, and all interest founders in a whirl of bewilderment. Agitating problems as to the difference between *Omphalotrochus discors* and *O. rugosus* (species beloved of the examiner) have little real value, even if solved, since both forms occur together in the Wenlock Limestone; while even the family distinction between Actinocrinidae and Amphoracrinidae has no greater stratigraphical significance. Is it not more useful, and less provocative of "cramming," to show that the wrinkled Turbinidae abound in the Silurian, and the smooth Euomphalidae in the Carboniferous; while the Actinocrinoida are wholly characteristic of the latter period? The most elementary student ought to know that Ammonites are not found in Cainozoic rocks; but he ought *not* to know the difference between *Dactylioceras commune* and *Peronoceras annulatum*. If the latter detail has been forced into his unprepared mind, some point of more general application and greater importance must have been omitted or ejected.

(B) PHYSIOGRAPHICAL

Indications afforded by fossils as to the conditions prevalent at the time and place of their life are hardly less important than their chronological evidence. Although it is unsafe to assume that past members of a group of

animals necessarily selected the same kind of surroundings as those favoured by their descendants, reliance can usually be placed on adaptive morphological features. The latter basis for argument has a further advantage, since it can be recognized in entirely extinct forms. There is still room for doubt as to the precise systematic position of the Tabulate "Corals"; but the correspondence of their general structure with that of living Madreporaria makes similarity of habitat more than probable. Again, the true Coelenterate affinities of the Graptolites are not securely established, but there can be no reasonable hesitation in ascribing to these extinct animals habits of life like those adopted by recent Hydrozoa and Polyzoa possessing comparable morphological features.

Just as some living Invertebrate types are known to be capable of maintaining vitality under a variety of conditions, or in spite of relatively sudden changes of environment, so some kinds of fossils may not imply definite physiographical qualities for the stratum in which they occur. As a general rule, the more highly specialized groups are sensitive to change; simpler types are more adaptable. The distinction applies equally in human affairs: a general education enables its survivor to lay his hand to almost any available work, the specialist is incapable of success beyond his particular sphere.

Lastly, it must be remembered that the relics of organisms may often be drifted into very different physiographical provinces from those essential for the life of their owners, and may become embedded in inappropriate matrices among strange companions. The frequent occurrence of fossil-wood in the Forest Marble and Lower Greensand could never be used as evidence that Conifers once grew in oyster-beds; similarly the presence of fresh-water shells mingled with those of

marine types must be ascribed to confusion of faunas by transporting agents. Further, discovery of Graptolites in black shales whose abysmal origin seems probable is no proof of the benthic habitat of those organisms. Their occurrence in such deposits is probably due to the sinking of planktonic surface-dwellers when buoyancy was lost.

(I) TERRESTRIAL FAUNAS

The rarity of fossils in terrestrial deposits is particularly marked in respect of Invertebrates. Only two phyla, the Mollusca and Arthropoda, are generally available for fossilization on land, and their representatives are confined to relatively few types endowed with somewhat delicate shells. The dominant terrestrial members of the two phyla are the Gastropoda and Insecta; in the case of the former an exiguous proportion only are Pulmonate. The average "snail" has a less massive shell than a marine Gastropod; and "slugs" secrete so little calcareous matter that preservation and discovery of their remains must always be doubtful. Except in the uppermost layers of the soil, dead snail-shells are rarely found, owing to the ready access of bacterial and aqueous agents of destruction. They may occur in considerable numbers in fresh-water deposits whither they have been drifted by streams; but in such cases they have passed out of their true province, and serve only to indicate the proximity of land to the place of their burial. To their extreme rarity in sub-aërial deposits a further contributory factor exists in the usually desert origin of geologically permanent terrestrial accumulations. Moreover, in rocks of considerable antiquity, it is difficult to be certain of the "pulmonate" character of a Gastropod, since the outward form of the shell gives little guidance towards determination of "soft" anatomy.

The chitinous coverings of Insects and allied groups are, in respect of solubility, more durable than Molluscan shells; but their extreme brittleness and delicacy demand for preservation conditions of burial that occur rarely on a land-surface. Like snail-shells, elytra of beetles are common in superficial soil, but such deposits only occasionally persist beyond the limits of the Holocene. Exceptions are found in the layers of soil covered by basalt-flows in Antrim, and in the "forest-beds" of the Purbeck and Pliocene. The not infrequent occurrence of Arthropod remains in the Coal Measures may be cited, but these nodule-cased relics had usually drifted into water before preservation was accomplished. Similarly the "beetle-cases" of the Great Oolite (especially the Stonesfield Slate) no more prove the sub-aërial origin of the deposits (often replete with marine fossils) than the discovery of Pterodactyle bones in the Chalk indicates either terrestrial formation for that rock or hydroplane habits for the Reptiles. Scorpion remains in the Trias are more reliable indices of the desert-conditions prevalent during that period, but even those are found usually embedded in layers suggesting the presence of local swamps or lagoons.

(II) FLUVIATILE AND LACUSTRINE FAUNAS

To a less degree than terrestrial faunas, those of fresh-water are lacking in variety and durability. Mollusca and Arthropods are still the dominant groups, but Pelecypods support the Gastropods (still mostly Pulmonates), while Ostracods and Crustaceans replace the Insects. The chances for fossilization of organisms in such surroundings are incomparably better than those for terrestrial forms, but the porous and transitory nature that belongs to most fluviatile deposits militates

against permanence of preservation. The process of filtration that converts alluvium into gravel involves exposure of shells to the devastating action of percolating water (by which even Mammoths' tusks are destroyed) while an ordinary gravel terrace assumes in time a position so exposed that its removal by denudation is well-nigh certain. The remains of fluviatile organisms can only attain lasting preservation when drifted into a lake or sea, and the vicissitudes of their journey are consistently destructive.

Swamp- or lake-deposits usually possess some virtue of constancy, and normally accumulate under very tranquil conditions. They are often argillaceous, and sometimes peaty, affording fairly safe burial to calcareous shells. In the case of aquatic Molluscs of high antiquity, the same uncertainty as to adaptive structure exists as in terrestrial forms; it is more from evidence of their associates than from any intrinsic qualities that *Archanodon* from the Old Red Sandstone or *Carbonicola* from the Coal Measures are regarded as fresh-water mussels. The Unionidae of the Yorkshire Jurassic, the Cyrenidae of the Wealden, and the Limnaeidae of the Oligocene give more certain indications of the lacustrine or deltaic conditions of their surroundings, since they clearly represent groups whose present distribution is of that nature. Shell-marls, often interbedded with peat, are frequent in the later Tertiary deposits, and in most cases mark lacustrine phases of sedimentation.

The Arthropods inhabiting fresh-water are usually small, and belong, for the most part, to groups equally, or better, represented in marine faunas. There is little difference in the shells or carapaces of members of allied groups inhabiting the two provinces. Among Ostracoda, the Cypridae usually prefer fresh water; their remains are particularly abundant in the deltaic parts of

the Wealden. Perhaps the swarms of *Beyrichia* that characterize the uppermost parts of the Silurian may indicate the oncoming of Old Red Sandstone lake-conditions; but closely allied forms abound in the Upper Ordovician, where no such prospect seems probable. In any case, detailed and special knowledge of these small "bivalves" is required if marine forms (which are common in the Chalk) are to be distinguished from those of fresh water. In like manner, it would be difficult, from study of the carapace alone, to ascribe to a crayfish fluviatile, and to a lobster marine, habits of life.

Perhaps the most satisfactory palaeontological indications of either terrestrial or fresh-water origin for a deposit are of a negative type. If fossils occur in a stratum, and none of them belongs to exclusively marine groups, the prevalence of one or the other of the non-marine conditions may be presumed. While most fluviatile Invertebrates have near allies living in the sea, many phyla are absolutely restricted to the latter region. Again, while it is possible, and by no means unusual, for inland organisms to be drifted into the sea, the reverse process is so unlikely as to be practically negligible.

A very instructive case of faunal modification due to physiographical change occurs in the Upper Silurian rocks of Shropshire; a similar phenomenon (at almost the same horizon) has recently been recognized in America. In the grey flags of the Upper Ludlow series, Protrematous Brachiopods, such as *Orthis lunata* and *Chonetes striatella*, are present in extraordinary profusion (Pl. vi. fig. 1). They are accompanied by a subordinate Molluscan fauna, in which species of *Pterinea*, *Modiolopsis* and *Orthoceras* are the most abundant types. As the flags pass up towards the Downtonian sandstones, the proportions of the groups undergo reversal. Almost

the only Brachiopods are *Lingulae*; *Orthoceras* disappears, and the bulk of the fauna is composed of Pelecypods, with occasional Tubicolous Annelids and Eurypterid Arthropods. The "Ludlow Bone Bed" gives striking testimony to almost catastrophic changes at this stage, and in the true Downtonian that supervenes, even Pelecypods have gone; *Lingula* alone survives, represented by dwarfed forms such as *L. minima*. The micaceous strata of the Passage Beds enclose *L. cornea*, and then almost all palaeontological evidence is lost in the marls of Lake Monmouth. The gradual transition from marine, through brackish, to fresh-water conditions is very clearly shown in this faunal sequence. The higher Brachiopods are exclusively marine, and disappear at the first suspicion of "estuarine" contamination. Many Pelecypods (especially the Mytilidae, a group nearly related to *Modiolopsis*) are indifferent to dilution of sea-water, although they cannot survive when sweetness has been quite attained. The Cephalopods are as definitely marine as the Brachiopods; but *Lingula*, one of the simplest members of the latter phylum, may well have possessed the catholicity of taste common to most lowly forms. A somewhat similar sequence, carried out with other genera and in the reverse direction, can be traced through the Rhaetic faunas from the Tea Green Marls to the Lower Lias.

(III) MARINE FAUNAS

The life of the sea can be grouped broadly into two zones, each capable of further subdivision. The two main provinces correspond fairly closely with the detrital and pelagic zones of sedimentation respectively. Forms inhabiting the littoral belt can be separated into those demanding a "clean" environment, and those

flourishing in muddy or sandy water. The fauna of the open sea can be divided in accordance with depth into planktonic, or floating, and benthic, or abysmal, types. Fossil evidence is hardly needed for recognition of the state of purity of sea-water, since the lithology of the sediments is a sufficient guide. As a general rule, Sponges, Corals, Echinoderms (other than Heart-Urchins), Polyzoa and Brachiopods avoid muddy surroundings, while Molluscs and many kinds of Arthropods find food and happiness where the water is thick with falling silt. Cessation, or extreme slowness, of deposition often gives opportunity for the growth of boring or incrusting organisms; such forms frequently indicate non-sequence in apparently continuous sediments. Tubular perforations due to *Pholas*, and clusters of Ostreidae, indicate that the layers affected had attained a fair degree of hardness before overlying sediments were laid down.

Evidence of the depth at which deposits were formed is made uncertain by two independent conditions. Provided that their remains can resist solution, planktonic organisms may sink to the floors of abysses; so that more or less sedentary forms can alone be relied upon for determination of depth. There can be little doubt, however, that the restriction of an existing group to any particular vertical zone in the sea is no criterion of its past habitat. Most of the recent stalked Crinoids, and a large proportion of Brachiopods, occur in very deep water; but in the past, when these groups were in their prime, their distribution was far more varied, and even brought them within the tidal zone. There is a marked tendency for members of a waning class to retire to the relative quietude of the deep sea; but this tendency is not a definite rule, so that discovery of senescent types cannot, of itself, give proof of benthic

conditions. It is usually necessary to determine the bathymetric range of the fauna of each period by various means (largely inductive), and to apply that knowledge to the fossils of the period concerned. In this way interesting conclusions can be reached as to variations in the depth of the Chalk sea. Ammonoids and Gastropods are fairly abundant in the Lower Chalk, become rare in the Middle Chalk, reappear in great numbers in the Chalk-Rock, and practically disappear from the Upper Chalk. Their presence corresponds with the prevalence of relatively shallow water; and, for the Cretaceous period at least, they may be used as evidence for such conditions. Similarly, *Discoidea*, an Echinoid ancestral to modern "Cake-Urchins" and "Sand Dollars" (whose distribution is mainly littoral), occurs in the Lower Chalk, and is represented by minute species in the Middle Chalk; but it is entirely absent from higher zones in this country. In other districts, however, such as Southern France and Northern Africa, the genus and its allies are abundant throughout the Senonian, in deposits of less pelagic characters than the British Upper Chalk.

(IV) FOSSILS AS EVIDENCE OF CLIMATE

Uncertainty as to the habits of extinct types of Invertebrates, and virtual restriction of their remains to marine types, make attempts at climatic "reconstruction" of doubtful value when based on such evidence. Although reef-building Corals flourish in warm seas at present, there is no more reason to suppose that their past distribution was similarly determined than to regard Proboscidea as exclusively tropical forms. The Mammoth endures as a lasting warning against assumptions of this kind. In the case of relatively modern

faunas, some confidence can be attached to deductions with regard to climate, especially when shallow-water forms are concerned. Thus the Lower Tertiary Molluscs of England show a definitely subtropical facies, when compared with living types; those of the Oligocene suggest temperate conditions, while those of the Pliocene and Lower Pleistocene are distinctly arctic. In all cases, however, terrestrial organisms (especially plants) are more exposed to climatic influence than those inhabiting the sea, and therefore give more delicate and reliable indications of change.

It is characteristic of partly enclosed gulfs to develop "sour" qualities in tropical climates, owing to excessive local evaporation. Concentration of the sea-water (such as that commonly found in coral-lagoons) adversely affects the fauna, giving stunted races, prone to disease. Perhaps the small size of most fossils in the Magnesian Limestone (and in many Triassic dolomites on the Continent) may be ascribed to such circumstances, and so give indirect evidence of the climatic conditions prevalent in the two periods.

CHAPTER V

BIOLOGICAL PALAEONTOLOGY

IN the small space available it is impossible to discuss, or even to catalogue, the various biological problems towards whose solution Palaeontology can contribute. Since detailed reference to the many branches of such research is impracticable, an attempt has been made to give a general account of the broad outlines of phylogenetic evolution. Long and tedious study will be necessary before many of the propositions here made can be proved or disproved; any stimulus to such effort, with either intent, that may perchance proceed from this chapter, would amply justify inclusion of theoretical matter in an introductory essay. The whole chapter is intended to convey hints as to lines of investigation that cannot fail to prove profitable; it is in no sense an epitome of all that has been achieved towards elucidation of evolutionary problems.

(I) PHYLOGENY AND MORPHOGENY

The stratigraphical record, whose interpretation is ultimately based upon the incontrovertible evidence of superposition, repays in full the debt it owes to palaeontological principles, since it supplies a historical sequence for the faunas of successive periods. It is possible to trace the direction and progress of evolution in its operation through vast ages of time with confident knowledge that the order of events is established. In spite of the

imperfection of the palaeontological record, phyletic or morphogenetic conceptions inconsistent with the known order of appearance of the phenomena concerned must prove ill-founded, and cannot carry conviction.

Valuable though this evidence is, two complicating factors conspire to obscure the views of evolution afforded. In addition to obvious gaps in the record where periods, long or short, are locally unrepresented by sediments, the recurrent differences in lithology of most continuous stratigraphical series indicate physiological changes inimical to continuity of life. A stock may have originated on sandy beaches in a district where those deposits are no longer accessible; and it may have attained full differentiation before the period of which strata, containing its remains, have been preserved. So that in a varied rock-sequence, scraps of the evolutionary history of types inhabiting the several environments are alone available. Even later discovery, in distant regions, of suitable matrices accumulated at the time of inception of the stock, cannot be relied upon to supply the evidence needed; since most, if not all, new groups originate in restricted areas, extending their geographical range only in later stages of progress. It follows, therefore, that the beginnings, and to a less degree the last phases, of race-history must usually be lost; while continuous record of its acmaic episodes can be pieced together only from dislocated fragments of evidence obscured by local variation. In rock-systems representing long-continued sedimentation under relatively uniform conditions (such as the Chalk), fairly extended and continuous views of evolutionary sequence are possible; it is from study of records preserved under such circumstances that criteria can be deduced for correlating the disconnected fragments of evidence commonly available.

Besides complication produced by geological imperfections, intrinsic difficulties obscure the trend of evolution. Like a river-system flowing over a broad plain, the stream of organic progress is not confined within one channel, nor does it follow a direct course. It is no easier to identify the main current (if such can be said to exist) in a delta, than to distinguish between the divergencies and convergencies in evolutionary history. A general direction of progress can be assumed in the one case no less than in the other; but the bourne to which evolution is tending has not yet been attained, its source is somewhere in the *terra incognita* of the remote past, while the complexities revealed by every glimpse available demand close and detailed study before their relation to the main system can be appreciated. The guiding force that determines the flow of a river is that of gravitation; to that principle all observed features can be referred, and by it unseen qualities can be conjectured. But what is the controlling agent that steers the course of organic evolution? That one exists is beyond doubt; its nature and operation are, as yet, but dimly visible.

Just as a group of organisms is the sum of its individuals, so an "individual" is the sum of its organs. At any one time, a group may include precocious and backward members; every individual possesses structures in varying states of efficiency. The quality, or stage of evolution, attained by a stock must be calculated as the average for its components, above and below which the relatively scarce progressive and regressive members flourish or languish. A group is in the ascendant if the progressive members outnumber the regressive; it is decadent if the proportions are reversed, for the average must tend to move towards the predominant extreme. The degree of success reached by

an individual may be measured by the relative harmony with which its component structures collaborate. Hence a high stage of elaboration in one particular character may often prove inconvenient or fatal to an organism, if it fails to conform to the functional requirements of less progressive features. The name "individual" thus proves misleading when applied to an organism, since, although the presence of all its structures may be necessary for life (an infrequent and dangerous condition), each one of its organs can have some independence of development during "individual" growth and evolutionary history. From the standpoint of evolution, it is essential to regard an "individual" as divisible into its several structures.

The organism is the unit of the group, and the organ the unit of the "individual"; the relation of the two units to their respective compounds is in some measure dissimilar. Thus it follows that study of race-history and that of structural evolution must be in some degree independent. Hence the two words in the title of this section. Phylogeny is racial evolution, morphogeny that of structure. The two studies are as inseparable, and as distinct, as organisms and their component organs. Race-history can be traced only through the sequence of individuals; progress or reversion in the latter is indicated by the qualities of their morphological characters. It follows that morphogeny must supply the basis on which phylogeny can be reared. Similar relations exist between Morphology and Taxonomy. Systematic classification must be founded on morphological discovery; phylogenetic series cannot be traced until morphogenetic trends have been recognized. But it is inexpedient, in either case, to await completion of the foundations before erecting the superstructure. Provisional classification, subject to continual revision, is

necessary if morphological research is to be co-ordinated and made intelligible; tentative schemes of phylogeny serve as convenient, if imperfect, correlations of established data in morphogeny.

On Pl. vii, figs. 2-13 an attempt is made to indicate the nature of a morphogenetic sequence, and to show its relation to phylogeny. The apical systems of Irregular Echinoids undergo disorganization (in ontogeny and morphogeny) by retrogression of the periproct. The posterior genital plate is resorbed; the gap in the cycle, and the central area once occupied by the periproct, have to be filled. Figs. 2 and 3 show two Diademoid (Regular) types of apical system; in both the backward tendency of periproct-movement is appreciable, but does not disturb the genital and ocular rings. (The alternative arrows connecting these figures indicate uncertainty as to the morphogenetic relation of Diademine and Calycine systems.) In *Plesiechinus* (fig. 4), the morphogenetic (and apparently phylogenetic) ancestor of Irregular Echinoids, the periproct occupies the posterior part of the system, breaching the cycle and displacing the surviving plates. From this condition two main trends of recovery can be traced. In that shown by the sequence of figures 9-11, no attempt is made to restore the lost genital; its place, and the centre of the system, are filled by extension of the madreporic plate. A slight modification of this method (figs. 12 and 13) closes up the system after the periproct has passed to the rear, producing in its extreme phase an elongate apical system with alternating plates. The second trend of recovery is shown in figs. 5-8. Here a new plate is formed in the wake of the receding periproct; in course of time, it assumes the proportions and function of the missing genital. The centre of the system is filled by inward extension of the genitals,

the madreporite perforating them all. This morphogenetic progress can be traced in the phyletic sequence Holoctypoida \rightarrow Clypeastroida; the two types of evolution are manifestly coincident and contemporaneous, the former supplying true evidence of the course of the latter. But in the other morphogenetic lines such correspondence cannot be claimed. Although *Anorthopygus* \rightarrow Spatangidae may be a phyletic sequence, *Anorthopygus* \rightarrow *Conulus* is improbable; while apical systems more elongate than that of *Echinocorys* existed long before *Conulus* appeared. The sequence illustrated may well be that by which elaboration was attained; the examples used need not have been in a direct genealogical line.

(II) POST-LARVAL ONTOGENY AND MORPHOGENY

Embryology is one of the most fruitful and fascinating branches of biological research. Not only does it reveal the essential and fundamental unity of all living things by demonstration of their common origin from fertilized ova; but the process of ontogeny, or building of the individual, is shown to follow definite courses which, with sundry imperfections and irregularities, seem to correspond with the evolutionary history of the groups concerned. Recapitulation is by no means an infallible guide to phylogeny; the brevity of the period during which developments reminiscent of long-continued specialization are achieved demands omission of many stages; the compressed epitome sometimes departs from its true historical sequence, while new structures may appear in adaptation to larval environment. But embryological study is practically denied to a palaeontologist. Most larval stages are devoid of hard

structures, and almost all are so minute that preservation and isolation are unlikely. Further, in the rare cases when early developmental forms are discovered, it is usually impossible to determine the relationship between larva and adult, since it is too late to watch the growth of one into the other. Nevertheless, Palaeontology can make use of certain ontogenetic qualities in adult or adolescent organisms that, within restricted limits, give a kind of recapitulation.

There are two "laws of stages of development" recognized, but they differ chiefly in application and mode of expression. One, the "law of stages in ontogeny" (Hyatt), is merely an extension of that of recapitulation. It states that in young forms, stages occur which correspond with the adult stages of ancestral types; while in senile individuals, stages occur which may repeat, in reverse order, those found in the young, and are in some measure prophetic of coming changes in subsequent evolution of the group concerned. Expressed in a simpler form, the law states that recapitulation continues till maturity, and is followed by anticipation of future changes in the stock. Hence it follows that study of the complete life-history of an individual supplies an abridged epitome of the history of the group to which it belongs. The other law, that of "stages in morphogeny" (usually and originally called the "law of localized stages in development," Jackson), states that throughout the life of an individual, there occur in local structures stages comparable with those found in youth or senility, supplying evidence on racial evolution similar to that afforded by ontogenetic stages. In other words, the growth of separate structures or organs follows recapitulatory or anticipatory courses in some respects independent of the age of the individual.

Both of these hypotheses are capable of appreciation,

and verification, in palaeontological material. Although full series of growth-stages of species can rarely be collected, a large proportion of Invertebrates retain the products of their early growth throughout life, so that a single specimen can, by dissection or analysis, be made to yield evidence of its ontogeny. Thus Ammonites added successive whorls during life, but did not destroy the first-formed parts of the shell. By "unwrapping" an Ammonite (removing one chamber at a time) the whole post-larval history of shell-growth is gradually revealed in inverse order, until the protoconch is reached. Similarly, Gastropods display their successive ontogenetic characters, although the exposed position in which the early whorls are usually left (at the apex of the spire) often results in damage or removal. Pelecypods and Brachiopods show in the umbonal regions products of early shell-formation, and may occasionally retain their prodissoconchs or protegula. The basal part of the theca of a coral has the first simple arrangement of septa and dissepiments, while more advanced stages of complication can be traced upwards towards the calyx.

Post-larval ontogeny is replete with difficulties like those that complicate embryology. The short time available in individual life for "revision" of age-long evolutionary history results in compression, omission, and even disturbance of sequence, of stages passed through. Developments of late introduction may be impressed upon structures of primitive simplicity. Thus, while the usual type of Gastropod protoconch is a smooth, slightly coiled shell, features of ornament characteristic of more advanced specialization may occur upon it, as has been well shown by Grabau in the Fusidae. But in spite of complexities, the principle of ontogenetic stages gives generally satisfactory indication of phyletic

evolution. Beecher proved its value in great numbers of Brachiopods and Trilobites, while many authors have applied it to the study of Ammonites, Gastropods and Pelecypods. Faunal succession is available to confirm or disentangle the records of post-larval ontogeny.

In several Invertebrate groups, notably the Echinodermata, new structures which are practically repetitions of those already present are developed throughout life. In Crinoids, the stem is lengthened by addition of new columnals; in Echinoids, the corona increases in size partly by introduction of fresh plates around the margin of the apical system. Organisms with such modes of growth will always possess some "young" structures, however "old" the individuals may be. For example, the common Holoctypoid, *Plesiechinus ornatus* (Pl. vii. fig. 1) shows certain coronal plates at the apex that are small, simple, and in course of development. These morphogenetically neanic ossicles are, in most respects, similar to the corresponding structures produced in early stages of individual ontogeny. From the time of their introduction onwards, such plates progress in growth and elaboration until they attain a degree of specialization harmonizing with the ontogenetic stage of their owner. Study of the interambulacrum of an adult *Plesiechinus* shows that the plates near the peristome, which date from the early youth of the specimen, are small, and support few tubercles. They represent the slight advance of morphogenesis corresponding with the short progress made in ontogeny at the time when they constituted the whole area. As the columns are traced away from the peristome, the size and tubercular ornamentation of the plates show steady increase, until, at the mid-zone (half-way up the corona, Plate xv.), they exhibit the highest phase of morphological complexity proper

to interambulacral plates of the species. Above the mid-zone, the characters of the plates show steady simplification as they are followed towards the apical system, attaining eventually a morphogenetic phase hardly to be distinguished from that of the first post-larval plates.

The corona of an Echinoid thus presents two somewhat similar (though reversed) sequences of morphogenesis. The plates below (adoral to) the mid-zone show, with certain modifications, the actual stages of morphogeny as they progressed in company with ontogeny; those above that zone show morphogenetic stages that are independent, in some measure, of the growth of the individual. But the ontogenetically-late "young plates" rarely follow exactly the path of development taken by their forerunners. The adult or senescent state of the organism induces various accelerations and modifications in the character of the new plates; however, these features rarely produce complications greater than those normal to ontogenetic stages. Perhaps the most satisfactory quality of this "continuous" type of growth is its evidence for the phyletic stage of the species in which it occurs. In *Plesiechinus*, as in Regular Echinoids, increase in length of the columns is achieved by accretion of new plates at one end (the apicad) only. Hence the horizon of the "mid-zone" steadily rises during life. This means that each one of the plates between the mid-zone and the peristome has been, in earlier stages of ontogeny, a "mid-zonal" plate. Apart from minor modifications, it retains in perpetuity the "finished" state of morphogeny associated with the ontogenetic stage when it was at the mid-zone. It follows, then, that if the mid-zonal plates of an adult specimen are the most highly specialized in the corona, the species to which it belongs is either progressive or at

its acme. On the other hand, if the mid-zonal plates are less elaborate than some nearer the peristome, the species is regressive, in that the culmination of morphogenetic development is reached, and passed, before the animal is fully grown. Great care is needed in interpretation of records of this type, since secondary specialization due to local requirements often obscures the original structure. But with due precaution, study of morphogenetic stages of development may often lead to deductions that can be verified by independent evidence.

(III) SPECIALIZATION AND REGRESSION

Arguing from the observed features of ontogeny, it is possible to conceive that a group of animals, at its inception, may be capable of improvement, the stage of perfection being attained when general efficiency is acquired. But it is impossible to maintain separation between the organisms and their environment. Organs that would do good service in rocky surroundings would probably prove worthless on sand or ooze; and, since groups are liable to changes of habitat, either of their own accord or owing to physiographical influence, the efficiency of one period may become the imperfection of another. The Echinoidea may be cited in illustration of this phenomenon. A large proportion of the Palaeozoic "Sea-Urchins" had flexible tests, apparently suited for life amid yielding materials; some modern members of the group, with similar habitat, show corresponding characters. During Triassic times, the Echinoids seem to have changed their mode of life, choosing reefs and rocks as their environment. Exposure to waves demanded strength and rigidity of fabric, and "Perischoechinoid" flexibility was abandoned. Through-

out the Mesozoic and Cainozoic eras, steady improvements, along various lines, were introduced, until at the present day such forms as the Echinometridae may be considered thoroughly efficient for rock-dwelling habits. But soon after this course of evolution had been entered upon, some groups of Echinoids reverted to the sand-habitat of their ancestors. The specializations for reef life initiated and elaborated by the one series would have been useless, and even dangerous, for the other, so that a gradual return to qualities like those of Palaeozoic types was begun. If racial progress is to be measured by the degree of success attained in adaptation of an organism to its environment, *Colobocentrotus* of the southern coral-reefs, and *Echinocardium* of the British sand-flats, are equally progressive. But in structure the Echinometridae are far more elaborate than Palaeozoic Echinoids, while the Spatangidae, with all their complexity, show many "Perischoechinoid" features. Morphogenetically the former family is progressive (anagenetic), the latter regressive (catagenetic); in efficiency, both are equal. The solution of such an anomaly is probably to be found in recognition that choice of environment is a character indicative of evolutionary activity, no less than structural specialization. The preference shown by Liassic Irregular Echinoids for muddy or sandy surroundings was an expression of their catagenetic tendency; morphogenetic regression followed inevitably after that backward step.

In the distribution of living organisms there is a pronounced tendency for moribund or antiquated types to avoid positions involving exposure to danger or competition. Thus the stalked Crinoids, many Brachiopods, and *Pleurotomaria*, now exist in the sheltered seclusion of deep-water, although their more vigorous ancestors joined successfully in the struggle for life in littoral

zones. Similarly Conifers and Lycopods, for the most part, have abandoned competition with Angiosperms, and prefer to brave the elements on mountain tops or in high latitudes. With this evidence and by analogy with individual life, it seems reasonable to suppose that races of organisms demand some measure of shelter during early and late stages of their development, and join in the turmoil of robust activity only when racial vitality is at its height. Choice of a sheltered environment by a group whose ancestors flourished amid competition is equivalent to confession of failure; morphogenetic changes thus induced are rightly considered regressive, however they may harmonize with the new surroundings. Development of adiposity or arthritis is eminently appropriate for individuals whose chief desire is for rest; the diseases and the desire are both symptomatic of old age and coming dissolution.

Specialization can, therefore, be defined as modification of structure conducive to success of an organism in the most strenuous sectors of the battle-ground of life; regression as that connected with retirement to sheltered surroundings. Both trends of evolution may be largely adaptive, although both are probably influenced by intrinsic qualities of racial rise and decay. The definition is neither complete nor exclusive, but it serves as a useful datum whereby evolutionary trends may be provisionally correlated.

The Ammonites have long been recognized as a group affording an unusually complete and obvious example of racial life-history. Although there is room for difference of opinion as to the intrinsic or adaptive qualities of the various modifications found in the group, the general sequence of structural change is so regular and so oft-repeated, that it must be ascribed to some fundamental tendency. The straight, smooth, many-

chambered "Bactriticones" of the Palaeozoic ancestors of the class were of such a nature that considerable increase of size, or exposure to rough treatment, could not fail to result in fracture. Although the septa served in some degree as reinforcements to the hollow tubes, they could not, while remaining smooth and distant, prevent rupture across the cavities of the intervening chambers. Since increase of length of the shell was apparently a pre-determined necessity, mechanical efficiency could only be attained by profound modification of the Bactriticone. A coiled tube is less easily broken than a straight one; hence a progressive tendency to enrolment and involution was initiated. In this way tubular shells which, if straightened out, would be of unwieldy length and corresponding fragility, came to be accommodated in compact and mutually supporting whorls. Complication of the septa, leading to the production of increasingly elaborate suture-lines, added to the strength due to enrolment, since it became impossible to make a straight fracture across the tube without intersecting some part of an internal, corrugated lamina of shell. The two lines of specialization, accompanied by more or less irregular elaboration of superficial ornament, were progressively followed, in the phase of anagenesis of the class, from the Devonian to the Trias; in the latter period the Ammonites attained their acmaic stage, excelling in structural perfection, specific differentiation and world-wide distribution. But from the Triassic period onwards, one group after another showed signs of failure (the phase of catagenesis), and ultimately became extinct. The expression of degeneracy varied in different groups. Some, represented by such genera as *Rhabdoceras*, *Ancyloceras*, *Hamites* and *Scaphites* (Pl. xiv. fig. 8), retained, and even increased, the complexity of their septal corruga-

tions, but failed to achieve, or maintain, enrolment. This type of reversion culminated in the Cretaceous *Baculites*, which, apart from internal details, was essentially a secondary Bactriticone. Other groups, exemplified by the Pulchelliidae of the Cretaceous period, retained the "Ammoniticone" involution, but allowed their septa to revert to a degree of complication hardly greater than that of the "Goniatites." For example, the suture-line of *Tissotia*, from the Cenomanian, is hardly to be distinguished from that of *Ceratites*, from the Muschelkalk. Although either of these regressive developments may have been associated with environmental influence, their appearance seems constantly to have preceded extinction of the groups affected. Whether such groups perished in the Trias, or persisted until the final collapse of the class in the Cretaceous period, they usually displayed, in their latest members, reversion towards ancestral features. The condition has been aptly described as "second-childhood." It must be admitted, however, that certain apparent exceptions to this rule are known. For example, *Indoceras*, an Upper Cretaceous genus from India, is not merely an "Ammonite" in shape, but has septa which in some particulars rival those of the most elaborate Triassic types. The significance of this and similar cases is open to doubt; but, in spite of exceptions, regression during degeneracy seems a definite principle of evolution.

Two common features of specialization, increase in size and addition of shelly matter, are readily traceable in fossil material. The former quality is not so marked among Invertebrates as among Reptiles and Mammals, especially in the catagenetic stages of its over-development; the latter is very clearly shown in a great variety of groups. Both tendencies seem particularly liable to persist beyond the stage in which they make for

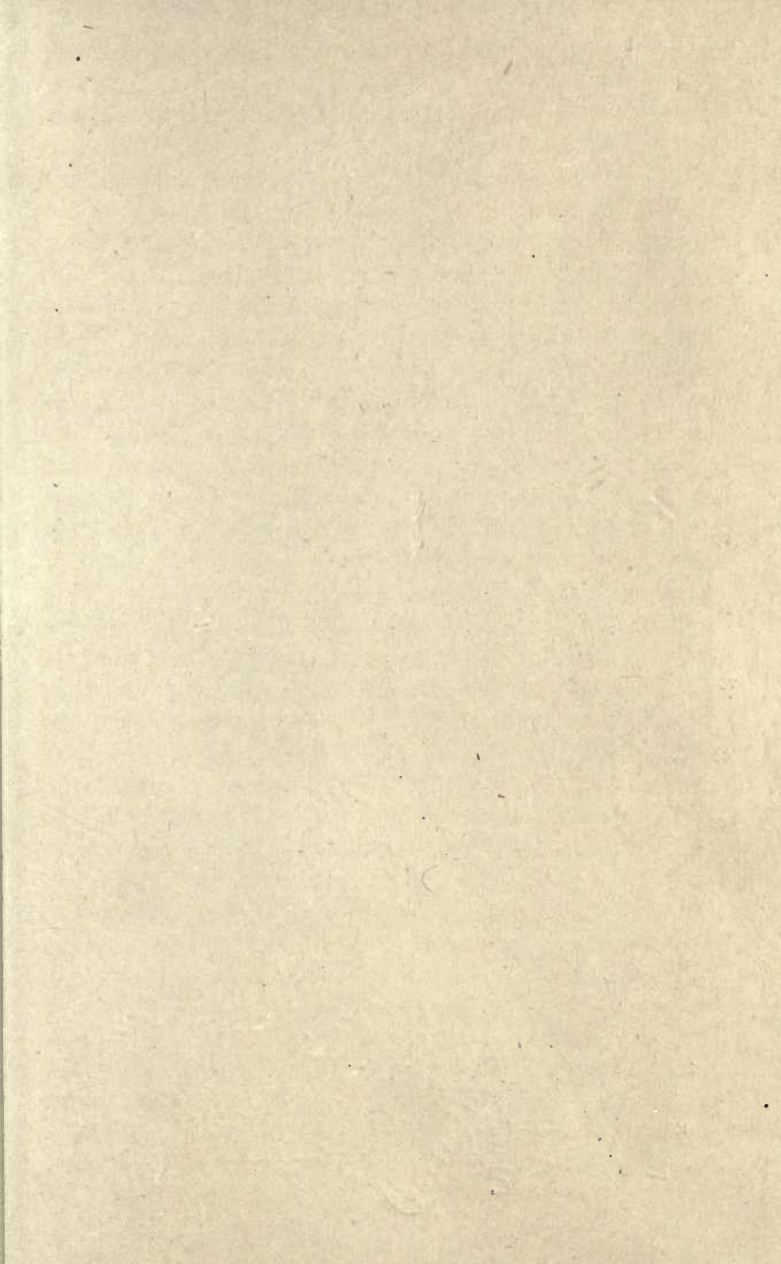


PLATE VII

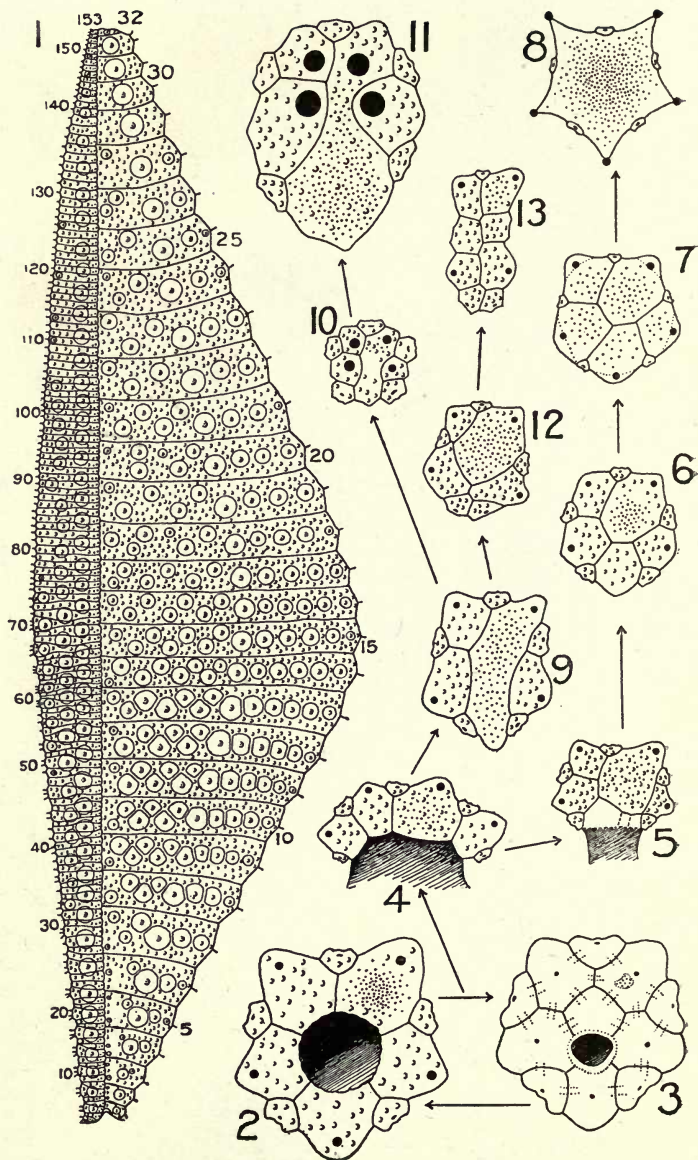


PLATE VII

FIG. 1. Diagram of contiguous halves of an interambulacrum and an ambulacrum of *Plesiechinus ornatus*, showing "localized stages in development." The first-formed plates (at the bottom of the figure), and the last-formed plates (at the top) show "youthful" characters of ornament. The full species-character is shown at the mid-zone.

FIGS. 2-13. Morphogeny of some types of apical systems in the Echinoidea.

Fig. 2. Diademine (e.g. *Hemipedina*). Fig. 3. Calycine (*Peltastes*). Fig. 4. *Plesiechinus*. Fig. 5. *Pygaster*. Fig. 6. *Holotypus*. Fig. 7. *Discoidea* (the posterior genital is not always perforated). Fig. 8. *Clypeaster*. Fig. 9. *Anorthopygus*. Fig. 10. *Spatangus* (after Lovén). Fig. 11. Adult *Spatangus* (after Lovén). Fig. 12. *Conulus*. Fig. 13. *Echinocorys*. For further explanation, see p. 94.

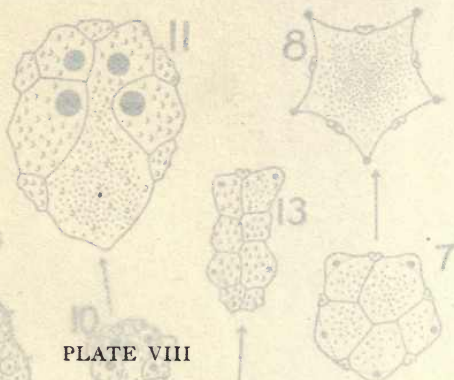
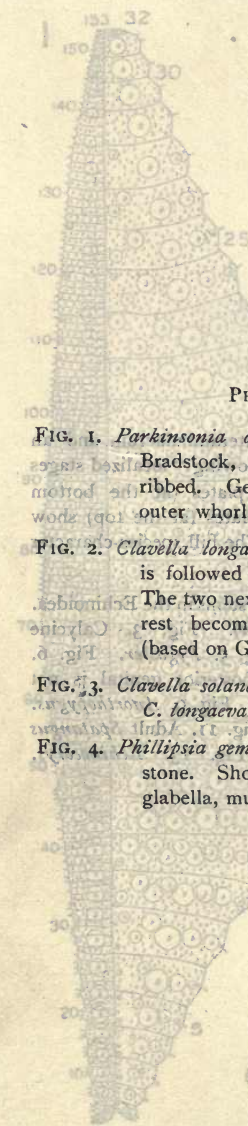


PLATE VIII

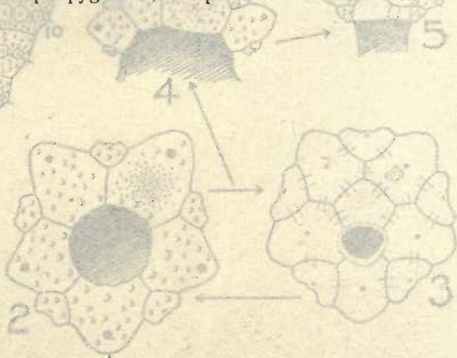
PHYLOGERONTIC CHARACTERS

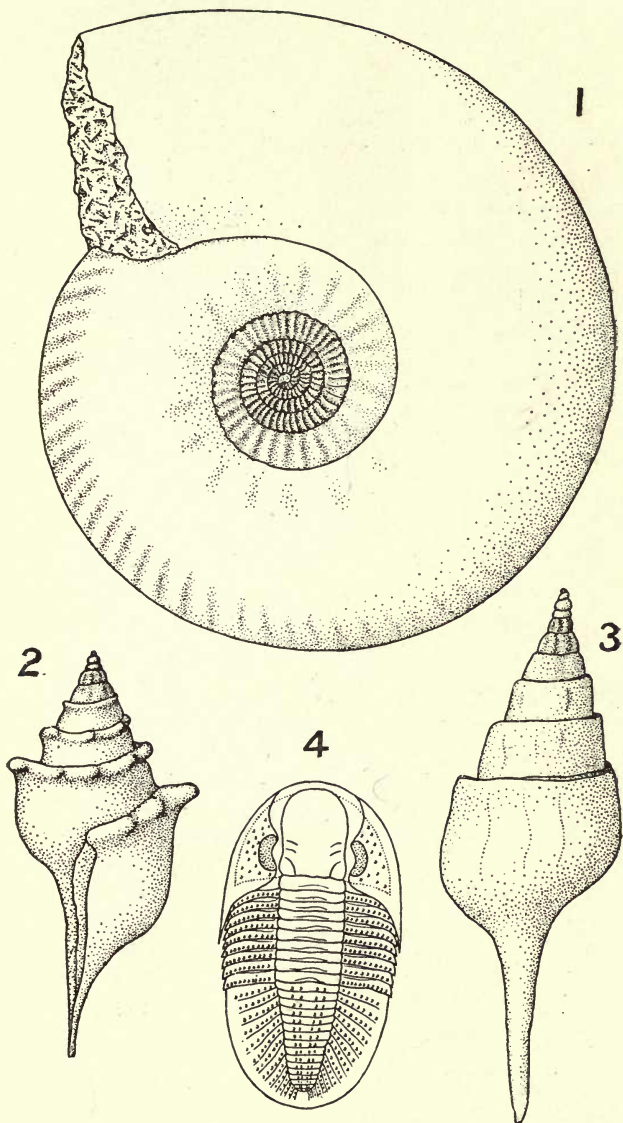
FIG. 1. *Parkinsonia dorsetensis* (much reduced). Bathonian, Burton Bradstock, Dorset. The inner (early) whorls are strongly ribbed. Gerontic laevigation obliterates ornament in the outer whorls.

FIG. 2. *Clavella longaeva*. Eocene, Barton, Hants. The protoconch is followed by one whorl showing "Fusid" cross-ornament. The two next whorls are smoothed by gerontic laevigation, the rest become secondarily spinous by excessive calcification (based on Grabau's figure).

FIG. 3. *Clavella solanderi*. Eocene, Barton, Hants. A type similar to *C. longaeva*, but failing to progress beyond laevigation.

FIG. 4. *Phillipsia gemmulifera* (after Woodward). Carboniferous Limestone. Showing gerontic features in simplification of the glabella, multiple pygidium, and pustular ornament.





efficiency. Among Mollusca, the Pelecypod family of the Pernidae produced, in Upper Cretaceous times (when the group was on the wane), species of *Inoceramus* that attained a diameter of about two feet, and secreted shells of a massiveness disproportionate even to that great size. Among Ammonites, such a name as *Pachydiscus peramplus* is sufficiently descriptive of comparable development towards the end of the life of the class. Excessive calcification is equally characteristic of "end-forms" in various groups. It may be shown in two ways, which seem, in some measure, antithetic. In some cases the superfluous secretion appears as warty or spinous outgrowths from shells whose ancestral types were relatively smooth. *Productus* (Pl. xi. fig. 6) illustrates this quality among the Brachiopods, while many species of *Spondylus* (particularly recent forms) may probably be claimed as examples of the same tendency. In other cases the additional mineral matter is spread uniformly over the outer surface of a shell, increasing its thickness and obliterating the ornament that characterized earlier members of the group. This "gerontic laevigation" is well shown in the later species of *Parkinsonia* among Ammonites, where the strongly ribbed character normal to the series is lost, in the outer whorls at least, in the massive shells of such types as *P. dorsetensis* (Pl. viii. fig. 1). *Clavella* (Pl. viii. figs. 2 and 3) shows a corresponding development among Fusid Gastropods. The aberrant types *Richthofenia* and *Hippurites* perhaps represent comparable phases in the degeneration of Brachiopod and Pelecypod stocks respectively.

There appear, then, to be two distinct methods whereby races of organisms may suffer extinction. In the regressive quality there seems to be a suggestion of some tendency akin to that of senescence; the group attains

its acme, and then descends along a course reminiscent of that by which it rose, dying of old age after a phase of second-childhood, when its vitality is exhausted. In the other case, over-specialization continues to produce effects which, after the acme has been passed, become positively disadvantageous in hypertrophy, however profitable they may have been in restrained development. But this "suicidal" tendency is none the less comparable with phenomena often shown in individual senescence. Morbid growths, either in bulk or sclerosis, frequently precede, and induce, death; so that the analogy between racial and individual life is still tenable.

(IV) ACCELERATION AND RETARDATION

The rate at which specialization proceeds varies to a marked degree in different groups of animals, and is not constant during the evolution of a single series; it may differ in the several parts of an "individual" organism. Some stocks seem born to stagnation, others to progress. The racial history of the former types tends to be long and uneventful, that of the latter short and crowded with morphogenetic episode. The contrast could hardly be displayed more clearly than in the case of the Tetrabranchiate Cephalopods already discussed. The Nautiloids, like the Ammonites, originated as forms with straight, chambered shells which have shown a steady tendency towards enrolment from Lower Palaeozoic times onwards. But whereas the Ammonoids attained the acme of their specialization in the Trias, and hastened to destruction in the Cretaceous period, the Nautiloids have not yet reached a degree of elaboration comparable with that of an Ammonite, and show no signs of aspiration to such an ideal. Although some

amount of enrolment was developed in that conservative group as early as the Carboniferous (while strong involution has characterized *Nautilus* since Jurassic times), the septa usually retain great simplicity. Not until the Cainozoic do corrugations comparable with those of Devonian "Goniatites" affect the Nautiloid septum, and even this small degree of complication has been abandoned by living forms. The different speed of evolution in these presumably homogenetic classes is associated with important results from a stratigraphical point of view. The Ammonoids appear in the Devonian, and disappear in the Cretaceous, attaining, in their relatively brief career, acmaic prominence of an extreme type. The Nautiloids arose in the Cambrian (or before), and are still living, but they cannot compare with their more progressive relatives in specific variety or numerical abundance. Their deliberate and unaspiring progress may be correlated with their early introduction. It is usual for the less-specialized, ancestral stocks of groups that have produced progressive branches to persist long after their precocious offspring have fallen from the acmaic heights. The Atrematous Brachiopods are represented to-day by species of *Lingula* remarkably like many of those prevalent in Ordovician seas; but the Orthacea, Strophomenacea and Spiriferacea, groups which seem certainly to have had an Atrematous ancestry, have had their day, and quite, or almost, ceased to be. The Echinoid family of the Cidaridae is represented by closely similar forms in the Lias and the Holocene, but many of the Jurassic and Cretaceous types, developed from the Cidarid stock and of far greater moment in their time, have been long extinct. Almost every phylum can show its conservatives and progressives; while the practically static qualities of those Protozoa whose palaeontological history can be

traced seems to indicate that the principle applies equally to large and small groups of organisms.

Tendency to specialization appears to vary in intensity and scope at different stages of racial evolution. There are three stages during which rapid morphogenetic acceleration typically occurs, coinciding fairly closely with the youthful, mature and senescent phases of race-life. Of these, the first is the most strongly marked, and is usually productive of the most far-reaching innovations. When the geological ranges of the several classes of a phylum are compared, it is commonly found that, while the periods of acme or extinction may be very diverse, the times of inception follow very shortly after differentiation of the whole group. In the case of most Invertebrate phyla, this quality is obscured by its pre-Cambrian remoteness, but among Vertebrates it is very apparent. The rich variety of the Cambrian fauna can doubtless be ascribed to its operation. That the same tendency works through smaller divisions is abundantly manifest. Indeed, the rarity of cases where gradual transition from one family to another can be demonstrated used to supply some of the most powerful arguments of opponents of the evolution-theory. However, analogy with individual life would make such neanic acceleration postulated, were it not actually observed. The early ontogenetic phases of an organism are plastic and protean, as one structure after another is produced and developed; relative stability characterizes maturity.

Among the many instances of rapidity of specialization in young groups, that shown by the Echinoidea is well marked. After a series of experiments in Palaeozoic times, the class acquired a certain fixity of character in the Triassic Cidaridae. (The Perischoechnoidea, in their manifold and extraordinary varieties, can perhaps

be claimed as neanic expressions of morphological exuberance.) Before the Liassic period ended, the Cidaridae were accompanied by representatives of at least two important families of Diademoida (Centrechionoida), and by the precursors of two distinct orders of Irregular Echinoids. Although many new types of Sea-Urchins have arisen since the Lower Jurassic, there is no evidence of later, almost synchronous, outbreaks of specialization comparable with that of the early Mesozoic. Among the Brachiopods three of the four orders were certainly differentiated in the Cambrian, and the fourth is well represented in the Ordovician, possibly passing back to the preceding period. Of the fourteen superfamilies into which the four orders are divided, seven date from the Cambrian, six from the Ordovician, and one only from the Devonian. All known families of the phylum were in existence in Palaeozoic times, thirty-four appearing in the Lower Palaeozoic and eight in the Upper. Similarly the Ammonoids were differentiated into two suborders before the close of the Devonian period. One of these, the Intrasisphonata, proved unsuccessful, but no later specialization in the more efficient Extrasiphonata produced modifications of subordinal importance.

A phylogenetic table of any group of organisms, particularly of the larger sections, resembles a bush in the abundance of branches arising from the root-stock. It could not rightly be called a "genealogical tree."

Following after the neanic differentiation of orders and families comes a phase of relative stagnation. Those early modifications that proved unsatisfactory drop out one by one, while successful developments are slowly improved and stereotyped. The adolescent phylum consists of a series of variously divergent lines rising to the acme. Each line may have its own rate of

progress, attaining its prime after an interval longer or shorter than that of its fellows; but there is commonly some measure of similarity in the quality of structural evolution in any homogenetic series. Such correspondence has been indicated above in the case of the Tetra-branchiate Cephalopods. The Nautiloids, in spite of the extreme deliberation of their progress, pursued lines of specialization which can be correlated with those precipitately followed by the Ammonoids. The principle of parallelism of development in homogenetic forms (orthogenesis) seems applicable to all grades of classification. Cases are not wanting where this morphogenetic correspondence is emphasized by its contemporaneous occurrence in divergent stocks. Among the Echinoidea several such phenomena occur. The Holoctypoid genus *Pileus* and the Diademoid family of Diplopodiidae—types ultimately homogenetic, but strikingly dissimilar in structure and probably in habitat—both show the unusual feature of biserial pore-arrangement adapically, and both arose in the Upper Jurassic. Again, the curious form *Lanieria*, an Holoctypoid with many affinities to *Holoctypus*, acquired in Upper Cretaceous times a type of ambulacral structure identical with that of the contemporaneous *Conulus*, with which it has few other features in common. This case is made more striking by the occurrence in the Lower Cretaceous of the Lanieriid genus *Discholectypus*, with similar ambulacral plating. *Discholectypus* can hardly be ancestral to *Lanieria*, but its development of *Conulus*-like structure coincides in time with the origin of the *Pyrina*-stock, from which *Conulus* is clearly descended. The Nucleolitoid genus *Trematopygus*, whose phyletic connexion with the Holoctypoida must be very remote, produced almost exactly the same type of structure in Lower Cretaceous times.

The second acceleration of evolution occurs when a

group of organisms is approaching its acme. This outbreak of morphogenetic activity rarely, if ever, equals the earlier phase in energy or scope. Differentiation of genera and species, rather than families or orders, marks its incidence. Since the acmaic stage is usually one in which the various members of a group excel in numerical wealth, it may well be that the separation of relatively small sections is an expression of the abundance of individual variation available for selection. Most genera or species evolved at the acme of a group are short-lived, though in their brief careers they may attain remarkable success. The types that survive to follow the descent of the group from its acme are usually those that took the least prominent part in acmaic specialization.

The third, and final, outburst of evolutionary activity occurs in the gerontic phase of a stock. Differentiation of ordinal quality is rarely developed at this stage, but new, often surprisingly aberrant, families may appear. Modifications of such importance that a rejuvenated stock is produced may occasionally be attained. An example of this phenomenon is probably afforded, among Vertebrata, by the Ophidia, which seem to range back no further than the Cretaceous period, when Reptiles as a class were on the wane. Perhaps the Sepioids are similarly related to the Belemnoids, and the Clypeastroids to the Holoctypoids. Usually, however, the families that branch from a gerontic stock show many features of racial old age even at their inception, and sink into oblivion together with their more orthodox associates.

The Brachiopoda may be cited afresh in illustration of the three stages of rapid specialization. The Telo-trematous superfamily Spiriferacea, whose relatively brief career lasted from Ordovician to Jurassic times,

reached a prominent acme in the Devonian. Of the nine families, no less than seven were differentiated in the Ordovician and Silurian periods. But the pre-Devonian genera number only twenty-four, whereas twenty-eight originated in the Devonian period alone; specific analysis would bring out yet more strongly the acmaic quality of minor differentiation at that time. Only twelve genera arose in the Carboniferous, and five in the Permian; but in the Trias, when the superfamily was approaching extinction, no less than twenty-one new genera appeared. In spite of this gerontic effort in specialization, the whole group disappeared before the end of the Liassic stage.

In addition to the differential rates of evolution indicated above (which are common to all, or almost all, series) there is a type of irregularity which, while as yet unrecognized in many groups, seems to modify the early phases of racial-life in several cases. It may be described as "deferred specialization." The outstanding example of this early retardation is to be found in the Mammalia. Although the Mammalian stock arose in Rhaetic, or perhaps Permo-Triassic, times, its members showed little progress throughout the Mesozoic era. At the commencement of the Cainozoic, extraordinary acceleration, typically "neanic" in character and products, rapidly brought the class into a position of faunal predominance. It is possible to argue, in this case, that the importance of Mesozoic Reptilia was such that there was no room for a second powerful group of Vertebrates; and it is true that the rise of Mammalia was deferred until the Reptilia were reduced to insignificant proportions in the fauna. But such an argument would in no way account for the slow specialization of the Mammalia. It might have been expected that the two great classes would have competed for mastery, the Mammals dissipating their racial energy in vain endeavours to make

headway against their Reptilian relatives. Unless patience prompted by some peculiar intelligence is to be attributed to early Mammalia, there must surely be assumed tendencies akin to precocity and backwardness in homogenetic groups. Just as precocity usually belies its early promise (however noteworthy premature progress may be), so backwardness is not infrequently followed by later acquirements that may lose nothing in brilliance because of their slow attainment.

Since the early phases of racial evolution are so imperfectly known in most Invertebrate phyla, the established case of the Mammalia may serve as an indication of the existence of the principle of "deferred specialization"; evidence of comparable qualities in Invertebrate phylogeny may be sought with confidence.

(V) THE LIFE-CURVE

Although the student of Nature may well stand aghast at the immensity and complexity of the problems and materials that lie before him, he finds, on closer inspection, that fundamental simplicity underlies the whole. After generations of study, resulting in a welter of observed facts and a chaos of abandoned hypotheses, a seer arises to show the single law whereby apparent confusion is resolved into an ordered scheme. In the physical sciences, phenomena are, for the most part, capable of reference to relatively few basic rules with almost mathematical precision; the results of experiment can in many cases be confidently foretold. In the various branches of Biology, something of the confusion that obscured the physical world before the advent of Newton still lingers. The principle of Evolution, like all broad conceptions, has served to co-ordinate, and so render intelligible, many of the manifestations of life, while the

older realization of the underlying uniformity that appertains to all living things was, in some ways, of even greater assistance towards understanding of vital phenomena. But there is not yet any real knowledge of the forces that drive, or the laws that guide, the stream of organic progress; a general view of faunas and floras, recent and fossil, gives an impression of a mob locally segregated into cliques rather than of a procession with definite order and aim. It may be taken as certain that the disorder is merely apparent—the product of imperfect and restricted knowledge. Palaeontology gives scope for longer and wider views than the Sciences that deal with existing forms alone; in fuller knowledge of fossils lies the hope for discovery of the fundamental laws of life.

In the earlier parts of this chapter, analogies have been made between individual and phyletic careers; comparison of the two kinds of "life-history" can be amplified with profit. It may be assumed that the laws that govern individual life are operative throughout the organic world. Such an assumption, supported by knowledge of the working of comparable laws, leads logically to the suggestion that a clue to the nature of vital principles may be found by study of the life-history of any single organism. Whether the expression of the laws manifested in the brief span of individual life is simplified, or concentrated (with resulting complexity), can be determined only by comparison with its extended record in phylogeny. But, since every organism gives some amount of phyletic recapitulation in ontogeny of the *matter* of which it is built, it is reasonable to expect that the *manner* and process of its living may bear comparable relation to the laws of evolution. "Know thyself" may still be the oracular reply to a seeker after biological knowledge.

There are four crises in the life of most animals, particularly of the Metazoa. The first, that of fertilization of the ovum, may be claimed as almost "creative" in effect; but its significance is far from clear, and the phenomena of parthenogenesis show that it is not universally necessary. The second crisis occurs after a period of larval or embryonic development, when metamorphosis, or birth, is reached. This normally takes place when ontogeny has produced some approximation to adult structure. The third crisis marks arrival at maturity, the fourth is death. In comparison with race-life, individual "birth" may be taken to represent the inception of a new stock, maturity corresponds with the acme, and death suggests extinction. By analogy, it is pardonable to speculate that fertilization is a "recapitulation" of the origin of life.

The crises are of relatively short duration; but they are clearly recognizable in phylogeny in all cases where reasonably complete knowledge is available. They serve as convenient divisions in developmental sequence of individual or group-life. The intervals between the crises vary much in length in different types of Metazoa; their duration is not necessarily commensurate with the amount of ontogenetic development attained. There is, however, a tendency for more highly specialized organisms to require longer periods for growth; though the phyletic "age" of the stock seems to have some influence.

The larval (or embryonic) stage of development is so clearly connected with phyletic evolution that it needs no further emphasis in this place. It is in the later phases of individual growth that comparisons with phylogeny are more feasible, in view of the nature of palaeontological evidence. Between birth and maturity, three stages in "anagenesis" can be arbitrarily separated

corresponding with infancy, childhood and adolescence. The episodes of these stages mark the progress of an organism towards the degree of development attained by the group of which it is a member. In common phraseology, a newborn infant may be said to "start late," so that it needs must "hurry" to catch up the main group of its fellows. But speedy as early progress may be, it leads along the same course that was taken during phyletic anagenesis of the stock. The dominant characteristics of youth can be ascribed to exuberant vitality. The child has to find its place in race-life, and to fit itself for the activities of maturity. Structurally it not only grows, but develops; psychologically it learns, chiefly by experiment, the only sound method. Habits, the subconscious sequels to experience, are acquired; some make for success, others may be harmful. If maturity is to bring full fruition, good habits must be confirmed and extended, bad ones dropped. The most enduring impressions are those gained in infancy; they are concerned with fundamentals, and their nature may influence the course of all later development of character. As childhood passes to adolescence, details are added to the early outline; the rate of their introduction becomes slower until maturity is reached.

It is clear that this sketch of early individual life could be applied, almost verbatim, to phyletic anagenesis, replacing the words infancy, childhood and adolescence by their phyletic equivalents neanic, nepionic and epacmaic stages. The rate and quality of differentiation in a stock are greatest in the neanic stage, when most ordinal (and even family) series are evolved. It is, moreover, particularly characteristic of this stage that great numbers of short-lived, often very aberrant, branches arise—the "unsuccessful experiments" of infant life. After neanic acceleration follows relatively

slow evolution, by which the selected types become gradually improved and are progressively endowed with those features that characterize the acmaic stage.

At maturity the individual has reached the forefront of its racial procession, and may progress a short distance beyond it. After a varying period of marching with the van, it tends, in typical cases, to slacken progress. But the race streams forward, so that the individual is left behind. Old age sets in; even if the attainments of maturity are kept, they soon prove to be "behind the times." Once again the individual is in the rear of the procession, but this time vitality is running low; efforts to "catch up" must end in failure. Various physical and mental qualities develop which are disadvantageous, almost without exception. Increase in bulk or sclerotic mineralization, often accompanied by degeneration of important organs (such as teeth), hasten and ensure the coming dissolution. But it is by no means rare to find that a strange reversion to tendencies reminiscent of early youth makes an inept appearance in old age. "Second-childhood" affords a grotesque and ponderous imitation of infancy, developed in combination with the worn-out aftermath of maturity. It seems to represent a final and despairing effort to regain lost ground by a new start. Like the final movement of Tscharkowsky's sixth Symphony, it marks a last, hopeless struggle before death brings peace and oblivion.

The catagenetic stages of phylogeny afford an almost startling parallel. The members of a phylogerontic stock are "born old," and show various modifications that are familiar in the senescent stages of individual life. Some types, such as the Proboscidea, grow unwieldy and, by reduction in the rate of reproduction, concentrate too much of the racial life into each individual body. Others, such as the Echinoidea (and

perhaps some Primates) suffer loss of dentition. Many show phyletic reversion, none the less analogous with second-childhood because incomplete. The Spiriferacea have already been cited in illustration of the outburst of specialization (of generic and even family quality) that precedes extinction; many other groups might have been used for the purpose.

It is possible, therefore, to summarize the matter included in this chapter by the suggestion that individual life does present, in epitome, the salient characters of phylogeny. The intensity of development varies in individuals no less than in groups. There are, roughly, two extreme types of individual life; that often recommended as "short and merry," and that "humdrum" existence that has usually been the lot of an "oldest inhabitant." Much may be accomplished during the brief course of the former type; little achievement, long drawn out, characterizes the latter. So in phylogeny the stocks that rise rapidly to prominent acmes fall precipitately; they have short, but effective, careers. Those groups that climb slowly and without distinction to inglorious maturity linger through an uneventful and protracted period of senescence. Accident may shorten, or shelter prolong, the lives of individuals; evidence is not wanting that comparable circumstances have influenced phyletic evolution.

Life, whether individual or racial, seems normally to follow a parabolic course. An organism rises from birth to maturity, and then, with like speed, sinks back to the unknown from whence it sprang. A phyletic stock pursues a similar course, anagenetic and catagenetic, from inception to extinction. The analogy is too perfect to be the outcome of mere coincidence or sophistry; it is an expression of the simplicity and order that are fundamental attributes of the Universal Cosmos.

PART II.—HISTORICAL BIOLOGY

CHAPTER I

PRE-CAMBRIAN FAUNAS

THE rocks that underlie the lowest beds of the Cambrian system cover a considerable part of the Earth's surface and attain an enormous thickness. They can be divided into two sections: a lower series of crystalline gneiss and schist, and an upper of less altered sedimentary and igneous material. Metamorphism has destroyed all original characters in the former series, so that there is little possibility of any palaeontological evidence remaining, especially since a large proportion seems to have been plutonic in character. *Eozoon*, once regarded as a reef-building Foraminiferan of Archaean times, has been definitely reclaimed from the Biological sphere, and proved to be a peculiar intergrowth of minerals in the crystalline complex of Opheicalcite. But while no determinable fossils can be expected in the "Laurentian" series of fundamental rocks, mineral matter suggestive of organic activity is not wanting. Masses of marble (crystalline calcite) and graphitic schists suggest the existence of limestones and carbonaceous shales among primeval deposits. However, knowledge of the conditions prevalent in Archaean times is so imperfect that it is at least as reasonable to ascribe these substances to inorganic precipitation or

distillation as to imagine that they are the products of life. The extreme scarcity of ooze-building animals and peat-making plants in the older fossiliferous strata lessens the probability of their occurrence in yet earlier periods.

Separated from the fundamental Archaean complex by a complete and intense unconformity, the pre-Cambrian rocks preserve, in the main, those lithological characters with which they were originally endowed. Greywackes, cleaved but hardly recrystallized, constitute the bulk of the non-volcanic parts; although the upper portions seem to consist of coarse arkose and conglomerate in most regions. Among British representatives of this system, the Uriconian (and comparable series) and Torridonian are unsuited for inclusion of palaeontological evidence, the former being mainly volcanic, and the latter probably terrestrial, in origin. But the slates of the Longmyndian series, interbedded with arenaceous and ashy beds, are not very different in lithology from much of the Lower Palaeozoic greywacke, and seem to have been deposited under comparable conditions. Worm-tracks and burrows, which occur in them, prove that the designation "Azoic" is inappropriate; but they have yielded no more satisfactory fossils. In America, a certain number of somewhat obscure forms have been discovered in the Algonkian (a formation not unlike the Longmyndian), but the interest of this discovery is a little discounted by the apparently Lower Cambrian facies of the fauna.

In spite of the almost complete absence of direct evidence, it may be taken as certain that organisms inhabited the pre-Cambrian seas. The wealth and variety of the Cambrian fauna demand preceding episodes of evolution; and yet, within itself, the fauna seems to indicate that its precursors would not have

been suited for preservation. Although most phyla, and a considerable proportion of orders, of Invertebrates are represented in the Cambrian, their numbers are few when compared with those known from the Ordovician. Fossils are locally common, even in the lower strata of the Cambrian system, but abundance is the attribute of an insignificant number of species. Extraordinary discoveries, such as those made in the Middle Cambrian of British Columbia, show that there was no lack of soft-bodied animals at that time; but such organisms are incapable of preservation under normal circumstances. Analysis of the fossils of the Cambrian suggests that chitin, rather than calcareous or siliceous matter, was the prevalent "reinforcing" substance; and chitin is usually too delicate in texture for satisfactory fossilization. The three groups of Invertebrates best represented in the Cambrian are the Brachiopods (chiefly *Atremata* and *Neotremata*), the Pteropods and the Trilobites. The lower orders of Brachiopods secrete shells which are largely corneous (e.g. *Lingula*), and the types prevalent in Cambrian times seem, on the whole, to have possessed this quality, with the additional character of smallness. The majority of the Pteropods ("sea-moths") are provided with excessively delicate shells, in which mineral matter is often entirely wanting. The Cambrian members of the group (e.g. *Hyolithes*), though possessing partly calcareous shells, seem to have been thinly clad. The Trilobites, like other Arthropods, had chitinous carapaces, in which only a small percentage of mineral matter was present.

Even the relatively scarce Cambrian representatives of other phyla usually show imperfect or flimsy mineralized structures, in striking contrast with the often massive shells and skeletons of their Ordovician

descendants. The rarity of fossils in Cambrian rocks may well be due to the inadequacy of contemporary skeletal tissue for preservation—it cannot be ascribed wholly to unsatisfactory lithological characters. It is therefore reasonable to suppose that the partial failure of palaeontological evidence in the Cambrian period gives (inverse) premonition of its total absence from earlier records. Not until the opening of the Palaeozoic era had evolution produced organisms capable of secreting “hard-parts.” Just as in ontogeny, early developmental stages are characterized by softness or delicate membranous coverings; so in phylogeny, the ancestral forms of a stock might be expected to lack structures capable of normal preservation.

The only Invertebrate phylum at present undiscovered in Cambrian strata is that of the Polyzoa. In all of the others, the types discovered are undoubtedly primitive in structure, although no indication of forms transitional between the phyla appears. The boundaries between orders are often obscure, but the essential characteristics of the great divisions had already been differentiated. The palaeontological record fails just where the most important events in evolution would be expected to appear.

It has often been argued that the occurrence of such diversity in the fauna of the Cambrian period requires invocation of a proportionately long sequence of previous faunas in pre-Cambrian times. But the methods of evolution that can be traced in later periods, and in smaller groups, must surely have operated consistently. It has been shown that the most striking characteristic of neanic phases of evolution is the rapidity with which important innovations (often of ordinal quality) are attained. Hence, the elaboration of the first Metazoan would probably be followed, in a relatively short time, by

differentiation of all the main phyletic stocks. The simple qualities shown by most Lower Cambrian organisms imply that the phyla were but newly specialized at that time. Perhaps some ancestral Metazoan stock had branched, almost at a single node, into the various phyla, at a stage not much more remote than the upper pre-Cambrian. Prior to this episode, comparable acceleration may have differentiated the three great sections of the animal kingdom within a relatively brief period.

It may be objected that the foregoing hypothesis is reactionary, in that it revives conceptions which, in geological discussions, have been discarded as unsound. Early schools of Geologists introduced ideas of the acceleration of physical processes in remote periods, largely under the (subconscious) pressure of theological prejudice. According to their beliefs, rain fell more heavily, rivers flowed more swiftly, and the sea (perhaps "boiling-hot") was more rapacious then than now, so that vast quantities of rock-matter were eroded and deposited during short intervals of time. All of which is not proven and difficult of belief. But arguments for organic acceleration fall into a different category. All available evidence points to the vigour and variability of youth, whether individual or racial. It is not mere speculation, but construction of a hypothesis based on observed phenomena, to suggest that differentiation and evolution of organisms may have proceeded rapidly (measured by later standards) "when the world was young."

CHAPTER II

LOWER PALAEOZOIC FAUNAS (PLS. IX. AND X.)

(A) GENERAL ACCOUNT

THE strata of the Cambrian, Ordovician and Silurian periods exhibit, in Britain, a certain monotony of lithological quality, relieved locally, and at various horizons, by development of volcanic rocks. These interludes were most widely distributed, and produced the greatest bulk of pyroclastic and other effusive materials, in the Ordovician period; but in spite of the scarcely fossiliferous nature of the Arenig series of Wales and the Borrowdale series of the Lake District, a practically continuous faunal record can be discerned, in one district or another, throughout the Lower Palaeozoic era. The dominant type of sediment is best expressed by the term "Greywacke"—detrital matter with an average composition of sandy slate containing small quantities of drifted volcanic ash. Actually all ordinary grades from conglomerate to pure clay-slate occur, but a certain argillaceous quality pervades the whole series, except in the north-west Highlands of Scotland. With the same exception, the few, relatively thin and impersistent, limestones of the series are usually earthy, even the coral-reefs being impregnated with grey shale. These limestones are either coralline or shelly; in no cases do they appear to represent deposits of the open sea. In many districts, notably the Welsh border and Anglesea, the

Lower Palaeozoic sediments are actually littoral in part, while in Southern Scotland the varied and inconstant physiography of a volcanic archipelago has left its mark upon the Ordovician and Lower Silurian deposits.

The geological history of Britain during the "Proterozoic" era can be summarized as follows. In Cambrian times a shallow sea, with a coast-line on the west, covered most of the district, and progressively extended its range westwards. Along a belt comprising Wales, the Lake District and parts of Southern Scotland, a very great volume of sediment was deposited, perhaps under the influence of a chain of islands (continuous with the Malvern axis) that converted that district into a partly enclosed sea. There was far less detrital matter available for sedimentation over central England. The deposits of the period show a transition from coarse arenaceous strata at the base to a remarkably uniform series of shales at the top. Isostatic depression more than kept pace with deposition, and created a deep but narrow geosynclinal along the central belt. The Ordovician period was marked by a decided reduction in the area of sedimentation, and a striking change in physiography. The rocks of this system seem almost restricted to the Wales-Southern Uplands belt, and include evidence of much contemporaneous volcanic activity. In Silurian times, after local upheavals, the sea once again spread over most of the British area (the Scottish Highlands excepted), once more receiving the most bulky deposits in Wales and the West of England. Towards the close of the Silurian period, important geographical changes were initiated; these culminated in the "Caledonian uplift," whereby most of the area was elevated beyond reach of the sea.

The forms of life predominant during the era were the Graptolites, Brachiopods and Trilobites. The first-named group arose in the later stages of the Cambrian, and became practically extinct before the end of the Silurian. During its short career it attained a very prominent acme; and by its rapid and abundant variation provided satisfactory zonal indices. Brief search in any Ordovician or Silurian shales usually reveals innumerable remains of Graptolites. The Brachiopods belonged chiefly to the three orders Atremata, Neotremata and Protremata. Of these, the two first were more abundant and varied during the Lower Palaeozoic than at any later stage; but they were overshadowed by the acmaic exuberance of the Orthacea, Strophomenidae and Pentameracea of the Protremata. It is rarely possible to visit a fossiliferous horizon in Proterozoic strata without discovery of many species that would have been called *Orthis* by early Palaeontologists; while Pentamerids are important rock-formers in the Silurian. The Trilobites are the most striking, and not the least characteristic, fossils of the Lower Palaeozoic. Hypoparia and Opisthoparia abound in the Cambrian, while the Proparia give them full support in the Ordovician. Although Trilobites range up to the Permian, post-Silurian types are usually scarce in occurrence and gerontic in character. The Ordovician is the period of their acme, twenty-two families (out of a total of twenty-eight) being there represented. Trilobites are used as zonal indices in the Cambrian (in the absence of Graptolites), but the world-wide range of many Ordovician and Silurian genera gives those later types great stratigraphical value, slightly discounted by tendencies to specific longevity.

(B) PROTOZOA

The relative simplicity of the Protozoa would suggest that they were abundant, if not predominant, members of early faunas. Although such a condition may have been realized, the fact remains that relics of the two orders capable of fossilization are less abundant in the Lower Palaeozoic than at later periods. Radiolaria occur sparingly in all three stages (and, indeed, in the pre-Cambrian), but Foraminifera are unknown in the Cambrian, barely recorded from the Ordovician, and exceedingly rare in the Silurian. Two explanations of this anomaly are available. The indurated quality of most Lower Palaeozoic rocks makes separation of minute fossils difficult; further, it has resulted from incipient metamorphic changes that would normally obscure small objects by molecular readjustment. The persistence of siliceous Radiolaria suggests the operation of this process, since their substance would offer resistance to alteration. Secondly, the retarded nature of Protozoan evolution may have found expression in delay in the secretion of hard structures. The almost complete absence of Foraminifera from Ordovician deposits seems explicable only on the assumption that few members of the order possessed durable tests at that time. Radiolaria are locally present in rock-forming quantities in the Ordovician of Scotland. Additional support for this belief is found in the nature of the least rare Silurian Foraminifera. *Saccamina* and *Placopsilina* are both "Agglutinantia," building tests in which adherent foreign particles are bound together by an insignificant amount of secreted matter. The few vitro-calcareous genera of the period are usually found as glauconitic moulds; while this character is shown even by Holocene types, it is suggestive of

speedy dissolution of very delicate tests. There are plenty of Silurian limestones which might be expected to afford complete preservation to calcareous Foraminifera if they had been available.

Among Radiolaria two suborders only, Spumellaria and Nassellaria, are clearly recognized in the fossil state. Of these, the former may with propriety be considered the more primitive, since its members are roughly spherical and have uniformly perforated skeletons. The Nassellaria, with diverse form and other specialized features, seem a more elaborate group. It is in accord with expectation to find that Lower Palaeozoic (and pre-Cambrian) Radiolaria are all Spumellarians. They are rarely well-preserved (their silica being usually devitrified into chert), and can be recognized in thin rock-sections rather than collected individually.

(C) PORIFERA

Two groups of Sponges secrete skeletal matter of durability sufficient for fossilization. Of these, the Silicispongiae tend to produce loosely associated spicules which collapse after death; Lithistids and Dictyonine Hexactinellids alone have well-knit skeletons. The Calcispongiae build relatively massive structures, and their preference for coastal waters gives them better chances of preservation than the usually deep-water Siliceous Sponges can attain. Nevertheless, Calcareous Sponges are unknown from the Lower Palaeozoic, while compact types of Silicispongiae occur in all formations from the Cambrian onwards.

Detached spicules of Monactinellid sponges appear first in the Silurian, but are rarely suited for precise generic diagnosis. Lithistids representing all five suborders occur in the Ordovician and Silurian; Tetra-

cladina alone (save for one genus) appeared in the Cambrian. Primitive Hexactinellids with disconnected spicules (Lyssacina) are not uncommon in deep-water deposits of the Lower Palaeozoic, the best known British genus being *Protospongia* from the Menevian. Long root-spicules of *Hyalostelia*, like those of recent "Glass-sponges," are also found.

The Receptaculitidae, a peculiar group of organisms of uncertain affinities, are fairly abundant in the Ordovician and Silurian. They are spheroidal or discoid bodies showing a "honeycomb" pattern externally. By various observers they have been classed as Calcareous Algae, Foraminifera and Echinoderms, but they are usually regarded as aberrant Porifera. *Ischadites* and *Sphaerospongia* are the chief British Lower Palaeozoic genera; the latter sometimes occurs in thick clusters in the Caradocian.

(D) COELENTERATA

A large proportion of Coelenterata are soft-bodied, and, although impressions of "Jelly Fish" and "Sea-Anemones" have been found in the Cambrian of British Columbia and the Upper Jurassic lithographic stone of Solenhofen, palaeontological evidence is normally restricted to a very limited series of forms. Of the two classes, Anthozoa and Hydrozoa, into which the phylum is divided, the former includes many types that secrete massive mineral structures, often attaining very great size (particularly in colonial forms). On the other hand, most Hydrozoa possess no skeletal tissue; or they secrete chitinous envelopes of great delicacy, giving but slight evidence of the distribution and nature of the soft parts.

Zoantharia (Corals) appear first in the Ordovician, except for the problematical Archaeocyathidae, which occur in the Cambrian, and have been recorded from yet

older strata. They immediately assumed biological and geological importance. Alcyonaria (or Octocoralla) have a like range, but are less satisfactorily known as fossils. Lower Palaeozoic Zoantharia belonged chiefly to two kinds, Tetracoralla ("Rugose Corals") and Tabulata. True Corals (in the recent sense) were wanting, unless the Archaeocyathidae belong to that group. The precise affinities of both sub-classes are doubtful, and recognition of the former is not universal. While Tetracorals have much in common with the later Hexacoralla (and may perhaps be an early and peculiar manifestation of that group), Tabulates, with rudimentary or absent septa, seem at first sight more akin to Alcyonaria or Hydrozoa. Both groups were important rock-builders in Lower Palaeozoic times, continuing through the Upper Palaeozoic and then becoming virtually extinct.

Relatively few Tetracorals are known from the Ordovician; small, solitary forms called *Petraia* are the most abundant. *Amplexus* and *Cyathophyllum* also occur, usually as small and simple species. In the Silurian an extremely rich series appeared. *Petraia* is still found in the Llandovery, while in the Wenlock Palaeocyclidae, Cyathophyllidae and Cystiphyllidae formed no inconsiderable bulk of the contemporary "coral-reefs." Solitary types (e.g. *Palaeocyclus*, *Cyathophyllum*, *Omphyma*, *Goniophyllum*) were accompanied by massive colonies (e.g. *Cyathophyllum*, *Strombodes* (Pl. ix. fig. 3), *Acervularia*).

Tabulates were undoubtedly the predominant group of Zoantharia in the Lower Palaeozoic. Favositids with massive, fungiform colonies (e.g. *Favosites*, *Alveolites*) are not uncommon in the Ordovician, and abound in the Silurian; Auloporidae, Syringoporidae and Halysitidae with recumbent or fasciolate habit are scarce at the lower horizon, but (especially the last-named) profuse in the Silurian. The fibrous Chaetetidae are also known from

these periods, but *Chaetetes* was more fully developed in the Upper Palaeozoic. *Favosites* (Pl. ix. fig. 4) and *Haly-sites* (Pl. ix. fig. 5) were the chief reef-builders of the era.

Alcyonaria were apparently represented by the abundant and short-lived family Heliolitidae. *Heliolites* persisted into the Devonian; the majority of genera were restricted to the Lower Palaeozoic, attaining chief prominence in the Silurian.

There are two series of Palaeozoic organisms referred to the Hydrozoa. Of these, the Stromatoporoidea have had a chequered systematic history, having been classed at various times as Calcareous Algae, Foraminifera, Porifera, Zoantharia and Polyzoa. Massive, "spongy," encrusting sheets of *Clathrodictyon* and *Stromatopora* play an important part in the construction of Silurian reefs, but the group was less abundant in the Lower Palaeozoic than in the succeeding era.

The Hydrozoan affinities of the Graptolitoidea are tolerably established, but they have been regarded as Plants, Porifera, Polyzoa and even Cephalopoda! Possessing wholly chitinous envelopes, Graptolites are rarely well-preserved, but this failing in no way detracts from their abundance and stratigraphical value. The two orders, Dendroida and Graptoloida, seem to illustrate evolutionary principles in a convincing manner. The former, with bush-like colonies supporting very small, simple thecae, arose in the Upper Cambrian (*Dictyonema*) and persisted to the Carboniferous, rarely attaining abundance and showing little modification. The latter, with less complex habit but far more elaborate thecae, appeared in the Ordovician, and, with the exception of one very rare type, became extinct in the Silurian. Owing to their short and varied career, and prominent acme, Graptoloida are of supreme importance as zonal indices in the two periods of their existence. Most

Ordovician types belong to the more primitive section Axonolipa (in which there is no continuous axis in the rhabdosome); the more specialized Axonophora persisted into the Silurian. Concurrently with this morphological trait occurs a habit that is readily recognizable. Ordovician types of both sections were either branched (all Axonolipa (Pl. ix. fig. 1), chiefly Arenig and Llandeilo) or "Diprionidian" (e.g. *Diplograptus*, *Glossograptus*). While both of these modes of growth were retained in the Lower Silurian, "Monoprionidian" forms (e.g. *Monograptus* (Pl. ix. fig. 2), *Rastrites*) are especially characteristic of that period.

(E) ECHINODERMATA

The Echinodermata, alone of Metazoan Invertebrates, secrete mesodermal skeletons which, like the analogous bones of Vertebrates, are intimately connected with the perishable organs of the body. Hence the phylum is peculiarly well-adapted for palaeontological study. The characteristic reticulate structure of the stereom is as distinctive as that of bony tissue, and makes even obscure fragments of Echinoderms recognizable as such. One class only, the Holothurioidea, is deficient in skeletal tissue; strangely enough remarkably well-preserved impressions of these forms are known from the Cambrian. Starfish and Brittle-Stars tend to have loosely constructed skeletons, so that their remains, though far from rare, are usually fragmentary. But the massive and coherent tests of most Echinoids, the bulky crowns and extensive columns of many Crinoids, and the compact thecae of Blastoids and advanced Cystids, give ample opportunities for fossilization.

Morphogeny and ontogeny alike indicate that the ultimate ancestors of the phylum were bilaterally

symmetrical animals. By adoption of sessile habits, more or less perfect radial symmetry (usually pentamerous) was acquired, and all but obliterated the early bilateralism. Many forms, by return to a free mode of life, superposed a fresh bilateral symmetry upon the radial one, but rarely succeeded in masking it completely. The primitive, bilateral stage is not known among fossils, although some of the early Cystids approach it very nearly. Probably the phylembryonic ancestors were without hard-parts, or provided with loose, delicate plates and spicules unsuited for fossilization. Certainly they must have lived in pre-Cambrian times. The sessile stage was brought to perfection in Palaeozoic times, and is all but abandoned in the recent Echinoderm fauna. Secondary freedom seems to have been attained very early, for some of its possessors are known from the Cambrian; but the quality is particularly characteristic of Mesozoic and Cainozoic forms. Palaeontological evidence is thus in accord with inference drawn from ontogeny and comparative morphology—the Pelmatozoa (sessile forms) are, in the main, older than the Eleutherozoa. The quality is well demonstrated by the proportions of attached and free classes now living. Three groups of Eleutherozoa (Holothurioidea, Stellerioidea and Echinoidea) are perhaps more abundant in recent seas than as fossils, the Edrioasteroidea (permanently or temporarily sessile types usually classed with the Pelmatozoa) closed their brief career in the Carboniferous period. But of the three classes of Pelmatozoa (Cystidea, Blastoidea and Crinoidea) Crinoids alone have survived the Palaeozoic era, and an overwhelming majority of modern types are eleutherozoic in habit, though not in structure.

Cystidea and Crinoidea were the predominant Echinoderms of the Lower Palaeozoic. The former class

was almost restricted to that stage, disappearing in the Lower Devonian. Both groups were represented in the Lower Cambrian, but the early Cystids were obviously the retarded survivors of a far more primitive stock than the Crinoids. The simplest Cystid order (Amphoridea) may well be regarded as morphogenetically representative of the first stage in Echinoderm fixation. Most Amphoridea have ill-defined radial symmetry, being irregularly sac-like forms whose Echinodermal nature is apparent chiefly in stereom-mesh and possession of a water-vascular-system. *Aristocystis*, an Ordovician genus, is the least elaborate of known types; *Eocystis*, a Cambrian form found usually as dissociated plates, may show an early stage in the development of a coherent theca. The Ordovician *Dendrocystis* (Pl. ix. fig. 6) marks a great advance on the primitive condition, since it possesses a definite, partly tubular, stem and an arm-like outgrowth from the opposite pole. It has been found in the Caradocian of Girvan; but the most familiar British member of the order is *Placocystis*, from the Silurian. This is a curiously specialized late form, laterally compressed and showing diverse plating-characters on the two sides. A well-marked stem is present, and two slender spines seem to take the place of arms. The extraordinary *Cothurnocystis*, recently described from the Ordovician of Scotland, shares many of the features of *Placocystis*, but is unique in the phylum in having several "oral apertures." The strange specialization of these flattened forms is ascribed to recumbent habits of life.

The order Rhombifera includes the most familiar types of Cystids. It shows an advance in symmetry from the Amphoridean pattern, and, in later types, may possess almost "crinoidal" regularity of plating. A peculiar and universal feature in the order is possession

of stereom-folds matching on contiguous plates, and becoming localized into "pectinirhombs" in specialized forms. *Macrocystella*, a crinoid-like form with a long stem and five bifurcating arms, is not uncommon (as dissociated plates) in the Shineton Shales. The Ordovician Caryocrinidae show much superficial resemblance to Crinoids and Blastoids. *Echinosphaera*, an almost globular form with numerous "rhombiferous" plates, is fairly abundant in the Ordovician, but is rarely found entire in this country. Silurian Rhombifera show obscure parallelism with contemporaneous Amphoridea in shape. *Schizocystis* and *Lepadocrinus*, with recumbent "arms" suggestive of Blastoid ambulacra, are among the few Cystid genera found in good preservation in Britain. They occur in the Wenlock Limestone.

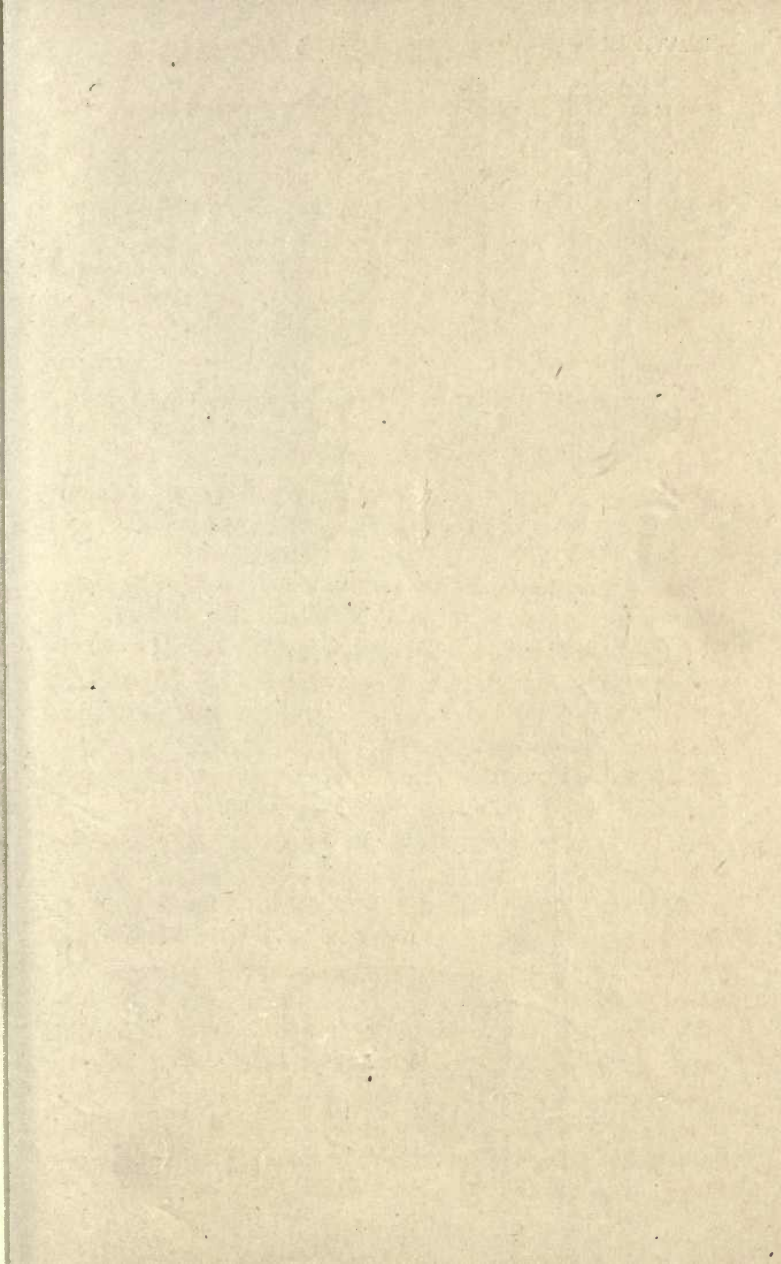
A small and inconspicuous order, the Aporita, occurs in the Ordovician and Silurian. *Cryptocrinus*, its typical representative, has a theca comparable with a crinoid calyx, but phyletic connexion between the two groups is very improbable.

The Diploporita, in which paired pores perforate the median stereom-layer, are perhaps the most interesting order of Cystids, since Blastoids were certainly derived through them, and there is reason to consider them ancestral to Crinoids as well. The order is essentially Ordovician in date, and seems clearly descended from the Amphoridea. The theca is usually globular or pentamerous in symmetry, with irregular plating (becoming more definitely arranged in later types) and food-grooves, terminating in brachioles, passing with increasing pentamerous regularity over the surfaces of the plates. *Sphaeronis* has food-grooves extending scarcely beyond the mouth; *Glyptosphaera* has five branching grooves passing for some distance over the theca. *Mesocystis* and *Proteroblastus* show a strong tendency to stereo-

typing of symmetry on the pentamerous plan, and local specialization of the plates traversed by the straight food-grooves. Both of these genera are almost as much Blastoids as Cystids; *Protocrinus* bears no small resemblance to some Edrioasteroids.

The last-named class (regarded by many as an order of Cystidea) seems to have been either extremely sessile (without stems), or imperfectly eleutherozoic (after the manner of limpets). Edrioasteroidea range from the Cambrian to the Carboniferous, and have been claimed as transitional between Pelmatozoa and Eleutherozoa. That they have strong Cystid (even Amphoridean) affinities seems certain, but in ambulacral structure they are definitely unlike the Pelmatozoa, and show a marked resemblance to eleutherozoic types. *Stromatocystis* is a Cambrian genus; *Edrioaster* typically Ordovician. *Hemicystis*, in the Silurian, foreshadows the scaly types characteristic of the Upper Palaeozoic.

The class of small Pelmatozoa named Blastoidea comprises forms that developed along "crinoidal" lines except in ambulacral characters. Instead of being raised on flexible arms, the food-grooves are recumbent, and pass with extreme regularity down five radii from the oral pole, sometimes almost reaching the opposite extremity (whence projects a slender stem). These "ambulacra" show strange superficial resemblance to the areas similarly named in Echinoidea; the comparison is amplified by the development of simple and "petaloid" structures. Primitive Blastoids (Protoblastoidea) are restricted to the Ordovician, and possess some diploporous plates, thus demonstrating their affinity with Cystid Diploporita. True Blastoids appeared first in the Silurian, where *Codaster* showed an early and incomplete phase of the development of internal stereom-folds (hydrospires) characteristic of typical families.



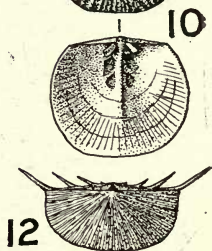
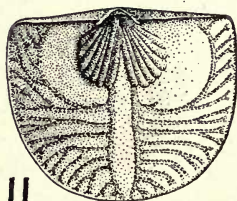
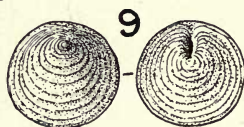
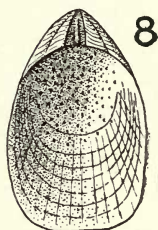
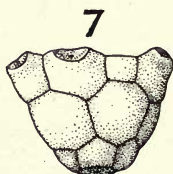
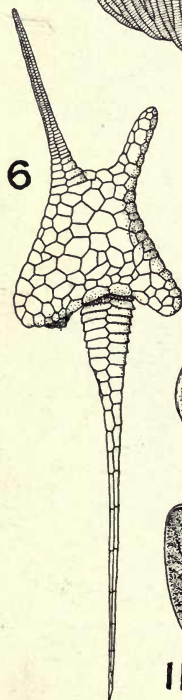
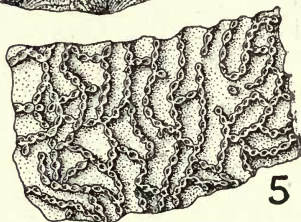
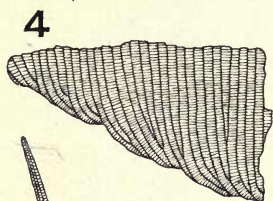
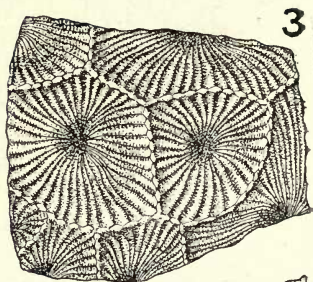
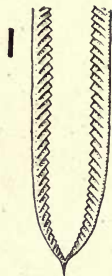


PLATE IX

LOWER PALAEOZOIC FOSSILS

- FIG. 1. *Didymograptus murchisoni*. Llandeilo, Abereddy.
- FIG. 2. *Monograptus sedgwicki*. Llandovery, near Girvan.
- FIG. 3. *Strombodes typus*. Wenlock Limestone, Much Wenlock.
- FIG. 4. *Favosites gothlandica* (longitudinal section). Wenlock Limestone, Presthope, Salop.
- FIG. 5. *Halysites catenularia*. Wenlock Limestone, Much Wenlock.
- FIG. 6. *Dendrocystis scotica* (after Bather). Caradocian.
- FIG. 7. *Cyathocrinus* sp. Wenlock Limestone, Much Wenlock.
- FIG. 8. *Lingulella davisi*. Cambrian, Tremadoc. (Partly based on Davidson's figure.)
- FIG. 9. *Orbiculoidea rugata*. Upper Ludlow, Onibury, Salop.
- FIG. 10. "Orthis" (? *Dalmanella*) *testudinaria*. Caradocian, Marshbrook, Salop. Restored from casts and moulds (see Pl. VI. Fig. 2).
- FIG. 11. *Strophomena expansa*. Caradocian, Soudley, Salop. Restored from mould of ventral valve (partly based on Davidson's figure).
- FIG. 12. *Chonetes striatella*. Upper Ludlow, Onibury, Salop.

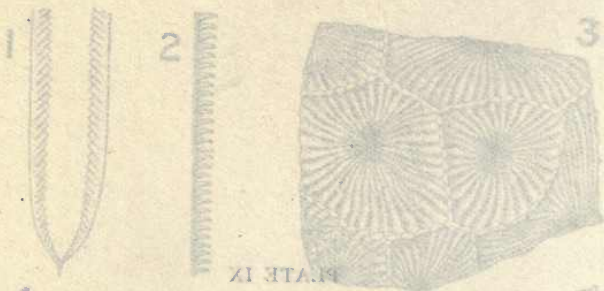


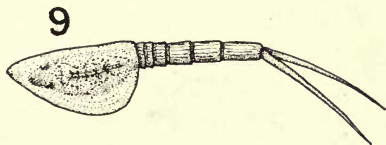
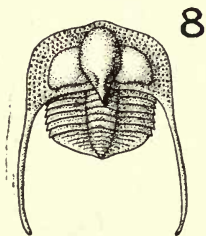
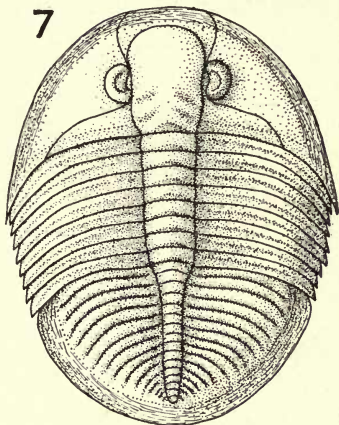
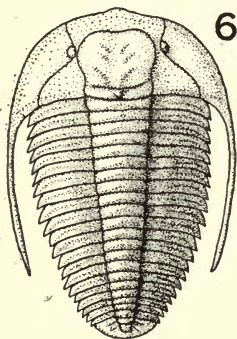
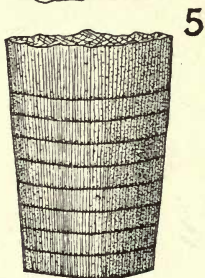
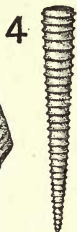
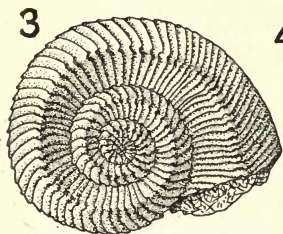
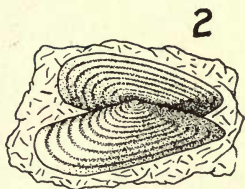
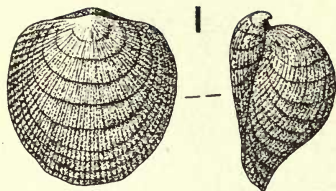
PLATE IX

PLATE X

LOWER PALAEOZOIC FOSSILS

- FIG. 1. *Atrypa reticularis*. Ludlow Limestone, Weo Edge, Salop.
- FIG. 2. *Orthonota rigida*. Lower Ludlow, Whettleton, Salop.
- FIG. 3. *Omphalotrochus discors*. Wenlock Limestone, Dudley.
- FIG. 4. *Tentaculites*. Caradocian, Marshbrook, Salop.
- FIG. 5. *Orthoceras bullatum*. Upper Ludlow, Onibury, Salop.
- FIG. 6. *Parabolinella triarthra*. Shineton Shales, Belswardine Brook, Salop. (Slightly restored.)
- FIG. 7. *Ogygiocaris buchi*. Llandeilo, Builth.
- FIG. 8. *Cryptolithus* ("Trinucleus") *concentricus*. Caradocian, Onny River, Wistanstow, Salop.
- FIG. 9. *Ceratiocaris* ? *leptodactylus*. Lower Ludlow, Martin's Shell, Leintwardine, Herefordshire.





Crinoidea, the only enduring class of Pelmatozoa, occurred in the Cambrian, but the oldest types are not well known. It is interesting to find that one Ordovician genus, *Hybocrinus*, had definite, though elementary, hydrospires, suggesting derivation of the class through, or parallel with, early Blastoid types. Extreme regularity in plating, and prolongation of the food-grooves on to "arms," are the dominant characteristics of the class. The calyx (patina) may be built of two or three cycles of plates; it is difficult to believe that the two characters (which imply contrasted arrangement of nervous and other structures) can have been developed more than once in Crinoid history. The two subclasses thus recognized, Monocyclica and Dicyclica, followed nearly parallel and synchronous courses of evolution, but Monocyclic forms are almost extinct to-day, while modified Dicyclic families are profusely represented in modern faunas.

Monocyclica are divided into three orders, Inadunata, Adunata and Camerata. The Inadunates, with calyces built of basals and radials (with or without intercalated anal plates), are known from the Cambrian, and still survive. They are generally small forms, and rarely prove abundant. *Hybocrinus*, from the Ordovician, has been mentioned above; the Silurian *Pisocrinus* is the only genus well known from British Lower Palaeozoic horizons. Adunata, with calyces like those of the Inadunata, but supporting massive tegmens, were mainly of Upper Palaeozoic date; but *Hapalocrinus* and *Marsipocrinus*, from the Wenlock Limestone, prepared the way for the abundant Platycrinidae of the Carboniferous Camerata, in which the calyx contains many incorporated arm-plates, were similar in stratigraphical range to the Adunata; *Periechocrinus* is a familiar Silurian forerunner of the later Actinocrinidae.

Dicyclic Crinoids are divided into Inadunata, Flexibilia and Camerata. The first and last orders are parallel, and practically contemporaneous, with the similarly named divisions of Monocyclica; an "Adunate" group might well be established for the Dicyclic *Crotalocrinidae*. Apart from the Silurian *Crotalocrinus* (one of the commonest of Wenlock Crinoids), *Cyathocrinus* (Pl. ix. fig. 7), *Gissocrinus*, *Petalocrinus* and *Dendrocrinus* are the most familiar Inadunate Dicyclica of the Lower Palaeozoic. *Reteocrinus* was an Ordovician precursor of the small, mostly Carboniferous, Camerate group. Flexibilia are chiefly Mesozoic and Recent forms, but *Taxocrinus* is not uncommon in the Wenlock Limestone.

Lower Palaeozoic Eleutherozoa are rarely abundant, and usually obscure. Wonderfully perfect impressions (almost amounting to petrifications) of apparently pelagic Holothurians, discovered in the Middle Cambrian of British Columbia, carry back the history of that debatable class to very early times. The two main sections of Stellerioidea (Asteroids and Ophiuroids) are both represented in the Lower Palaeozoic (the former in the Cambrian), but their collapsible nature makes interpretation of their structures and affinities difficult. The chief British Proterozoic deposits in which Stelleroids are at all numerous are thin layers in the Caradocian of Girvan and the Lower Ludlow of Leintwardine (Herefordshire). *Lapworthura*, an "Ophiuroid" form, is extraordinarily abundant in the latter "Starfish bed." Isolated occurrences in Ordovician and Silurian rocks of other British localities are not infrequent, but the usual obscurity of the fossils makes them unsuited for discussion in general terms.

The earliest recorded Echinoid is *Bothriocidaritis*, a small, subglobular form from the Ordovician. It differs from all other members of the class in having inter-

ambulacra built of single columns of plates, and ambulacra composed of a few high, hexagonal plates alternating, and agreeing in proportions, with the contiguous interambulacra. These qualities seem certainly primitive, since they are repeated in the early post-larval ontogeny of most later types; ancient and degenerate groups retain at least one single plate in each interambulacrum throughout life. Two Silurian genera, *Echinocystis* and *Palaeodiscus*, from the Leintwardine Starfish bed, are somewhat problematical; in their many-plated interambulacra and congested ambulacra they show progress towards normal "Perischoechinoid" characters, but their true phyletic position is undetermined. *Palaeoechinus*, a true Perischoechinoid genus, has been found in the Silurian, but reached fuller development in later periods.

(F) POLYZOA

The Polyzoa (or Bryozoa) are divided into two classes: Entoprocta, in which the circlet of tentacles (lophophore) surrounds both mouth and anus, and Ectoprocta, with the anus outside the lophophore. The latter class comprises the vast majority of known Polyzoa; it is further subdivided into the groups Phylactolaemata and Gymnolaemata. Save for certain problematical forms, all fossil types seem referable to the latter subclass. Polyzoa are usually abundant fossils at all horizons from the Ordovician (in which they first appear) to the Holocene; but their normally small size has occasioned relative neglect, with the result that their classification is as yet indefinite.

Of the five orders of Gymnolaemata usually recognized, four are known from the Ordovician, and two are virtually restricted to the Palaeozoic. The simple,

thread-like colonies of the Ctenostomata (e.g. *Vinella*) are more abundant in the Lower Palaeozoic than at later horizons, but they never attain prominence. Cyclostomata seem to be represented in the Ordovician and Silurian by the suborder Ceramoporoidea (e.g. *Ceramopora* and *Fistulipora*); these somewhat problematical forms constituted a large proportion of the Polyzoan fauna of those periods. The abundant series of forms known as Trepostomata are particularly characteristic of the Lower Palaeozoic (though enduring to the Permian). Under the name of "Monticuliporoids" their massive colonies were long regarded as those of Coelenterates of Alcyonarian affinities, but their Polyzoan position seems established. Cryptostomata, another exclusively Palaeozoic order, were less abundant in the Lower than in the Upper periods, but *Ptilodictya* sometimes occurs in profusion in the Ludlow Limestone. This order was most probably ancestral to the Cheilostomata, the predominant group of Tertiary and Recent Polyzoa, which are not known from the Palaeozoic.

(G) BRACHIOPODA

In clearness and completeness the palaeontological record of the Brachiopoda is superior to that available for any other phylum. Not only do all members of the group secrete shells suited for preservation, while retaining some evidence of "soft" anatomy; but there is reason to believe that the earliest Brachiopoda known are very nearly the simplest and most archaic of their kind. In the Cambrian Rustellacea there is perpetuated the primitive stage of evolution when adults were encased in shells hardly different (save in size) from the first post-larval "protegula" of later types. A large proportion of known Brachiopoda are not only fossil but

Palaeozoic; during that era they rivalled, in numbers and differentiation, the later achievements of Mollusca.

The simple, inarticulate, largely corneous order Atremata enjoyed in the Lower Palaeozoic such repressed prominence as it has attained. After the close of the Silurian period, but one family lingered to perpetuate the stock in the existing fauna. The exceedingly rapid, and relatively profuse, specialization of families in Cambrian and Ordovician times is suggestive of neanic acceleration; and, since the Atremata are undoubtedly ancestral to all other orders of Brachiopods, indicates a late pre-Cambrian stage as the time of inception of the phylum. The Lower Cambrian *Rustella* (unknown from Britain) cannot be far removed in morphology from the first definite Brachiopod. Its contemporary *Kutorgina* shows modifications pointing towards the Protremata. The most abundant family of Cambrian Brachiopods, the Obolidae, is represented by *Lingulella* (Pl. ix. fig. 8) in the middle and upper Cambrian of this country, and was continued into the Silurian by the massive, phylogerontic stock of the Trimerellids. Some early Obolids seem to have given rise to the Neotrematous group Obolellidae. It is probable, though less certain, that the same series of Atremata are on the direct line of descent of the Telotremata. The Lingulacea, destined to survive with scarcely any important modification until the present day, seem to be continuous with the Obolid group represented by *Lingulella*, appearing first, and in greatest profusion, in the Ordovician. *Lingula* itself was often exceedingly abundant in shallow Silurian seas, and attained much specific differentiation during that period. In particular, the beds of *Lingula cornea* and *L. minima* in the Uppermost Silurian are deserving of notice.

The small, curiously specialized members of the

Neotremata can be classed into four groups, two of which were restricted to the Lower Palaeozoic. The other two (Discinacea and Craniacea) did not appear until the Ordovician, and, like the contemporaneous Lingulids, have proved persistent, though showing their greatest differentiation in pre-Devonian times. *Acrotreta* is the best-known genus of Neotremata occurring in the British Cambrian and Ordovician; *Orbiculoidea* (Pl. ix. fig. 9) is equally familiar in the Wenlock and Ludlow stages of the Silurian.

Very few Protremata occur in the Cambrian, but archaic forms of Orthacea and Pentameracea are known. *Billingsella* and *Eoorthis* are the only types certainly recognized in Britain. In the Ordovician, the Orthidae arose and reached their acme. *Orthis* (Pl. ix. fig. 10), *Plectorthis* and *Hebertella* were abundant genera. Comparable acceleration was shown by the Strophomenidae, *Strophomena* (Pl. ix. fig. 11), *Rafinesquina* and *Plectambonites* occurring in great profusion in some beds of the Upper Ordovician. The first of the *Chonetes*—stock, from which the Upper Palaeozoic Productids were evolved, made its appearance in this period. Small Pentameracea, such as *Clitambonites* and *Porambonites*, are locally abundant. In the Silurian, the Orthacea and Strophomenacea continued the acmaic success attained in the previous period, *Plectorthis*, *Dalmanella* and *Bilobites* generously representing the former, and *Leptaena*, *Strophonella*, *Streptis* and *Chonetes* (Pl. ix. fig. 12) the latter. Pentamerids attained their acme in this period; the smooth *Pentamerus* forms beds of limestone in the Llandovery, the partly plicate *Gypidula* abounds in the Wenlock, and the large, evenly-ribbed *Conchidium* (Pl. ii. fig. 1) builds much of the Ludlow Limestone.

Telotremata are the least important order of Lower Palaeozoic Brachiopods; and, were it not for the

accelerated evolution of the short-lived Spiriferacea, would be almost negligible. A few primitive Rhynchonellids occur in the Ordovician, and the genera *Camarotoechia* (Pl. vi. fig. 1) and *Wilsonia* exhibited the true *Rhynchonella* type in the Silurian. No members of the Terebratulacea appeared until the Devonian. Spiriferacea were, without doubt, the most elaborate of Brachiopods. Ordovician types (with very few exceptions) agreed in having the brachidial spirals directed inwards, as in *Zygospira* and *Atrypa*. Most families originated in the Silurian. The true "Spirifers" are there represented by *Delthyris*, *Eospirifer* and *Cyrtia*, the relatively long-lived Suessiidae by *Cyrtina*, and the elaborate Meristellidae by all the acmaic complexity of such genera as *Nucleospira* and *Meristina*. *Atrypa* (Pl. x. fig. 1), surviving from the Ordovician, rivals *Conchidium* as an Upper Silurian rock-former.

(H) MOLLUSCA

No other phylum can show so voluminous a record as the Mollusca. Although subordinate to Brachiopoda in Palaeozoic times, the three classes Pelecypoda, Gastropoda and Cephalopoda reversed the proportions in an overwhelming manner in the Mesozoic, and certain groups of the two first series are only less abundant than Insects at the present day. A few types live on land, many in fresh water, and a multitude in the sea. Some marine forms are littoral, others pelagic; few are abysmal. Certain families flourish in the muddy water of estuaries, others prefer rocks or reefs. The majority of Molluscs secrete relatively massive shells, and, in spite of the preference for Aragonite shown by some groups, are better adapted for fossilization, by structure and habitat, than most other Invertebrates. In spite of

these excellent qualities, which result in abundance of palaeontological material, Mollusca are, in the main, unsatisfactory fossils. The shells are wholly external structures, and so usually fail to receive much impression from perishable morphological characters. Study of recent types shows that the features of chief importance in taxonomy are sensory, respiratory, reproductive and masticatory organs. All evidence of these qualities is usually inaccessible in fossil material, so that the classification of extinct Molluscs is inevitably somewhat empirical. Stern necessity, and fortunate coincidence, have made the Cephalopoda reveal characters of taxonomic value; it is probable that further researches on Pelecypods and Gastropods may make palaeontological classification possible. Moderately successful attempts have been made in the case of Bivalves, but Univalves are still grouped into families by analogy rather than morphology.

Of the five classes of Molluscs suitable for fossilization, Gastropods alone are definitely recognized in the Cambrian. It is possible that Pelecypods and Cephalopods may occur, but much uncertainty surrounds the obscure and primitive types recorded. Cambrian "Bivalves" have on several occasions proved to be Branchiopod Crustacea (or even distorted Brachiopods); while presumed *Orthoceras*-forms from that horizon might be ascribed to utterly different organisms with equal probability. Both Pelecypods and Cephalopods were represented in the Ordovician, where they were accompanied by the earliest Amphineura. Scaphopods possibly occur in the Silurian, but their simple tubular shells are difficult to distinguish from those of Pteropods or even Tubicolous Annelids.

The Pelecypoda are divided into three subclasses, Prionodesmacea, Anomalodesmacea and Teleodesmacea.

The two last-named series may possibly occur in the Ordovician, but Lower Palaeozoic forms are problematical and rare. Two genera, *Orthodontiscus* and *Allodesma*, are sometimes classed with the Teleodesmacea. They were probably Schizodont Prionodesmacea having possibly ancestral relations with the more elaborate group. Prionodesmacea were the chief bivalves of the Palaeozoic; their prominence in early faunas was due rather to the feeble development of the other two subclasses than to intrinsic abundance. In actual numbers Mesozoic forms exceeded many-fold those of the earlier era. An obscure series of Prionodesmaceans with unhinged valves (Palaeoconcha), ranging from the Silurian to the Holocene, is represented in the former period by a few forms, of which *Cardiola* is a familiar fossil of the Wenlock and Ludlow stages. The Taxodonts, which include forms whose primitive qualities can be assessed by dissection, appeared in the Ordovician. The two genera of chief interest are *Nucula* and *Leda*, both of which have persisted from the Silurian to the present day with remarkably little change. They clearly represent the "*Lingula*" type of evolution wherein early stocks are perpetuated by almost static morphogeny. The most important Schizodonts (a series that occurred in extreme profusion in the Mesozoic) were the radicals of the Pteriidae. *Pterinea* is common in the Upper Silurian, and can be found in the Ordovician; while *Rhombopteria*, claimed as the true morphogenetic ancestor of the family, was of Silurian date. Isodonts are represented by early forms of *Pterineopecten* in the Silurian, but are rare. The Dysodonts, so familiar under the name of "Mussels" at the present day, were perhaps the commonest series of Lower Palaeozoic Pelecypoda. *Modiolopsis* is not uncommon in the Ordovician, and

with *Orthonota* (? a Taxodont) abounds in the Ludlow series of the Upper Silurian (Pl. x. fig. 2).

Gastropoda are separated into two main sections (Streptoneura and Euthyneura) by the distribution of their chief nerve-trunks; classification of the next grade is based on qualities of the respiratory organs. Most smaller subdivisions are recognized by the nature of the radular teeth. It is clear, therefore, that inclusion of many fossil Univalves (especially early forms) in such orders and families must be tentative. As far as can be ascertained, both Streptoneura and Euthyneura formed part of the Cambrian fauna. Both sections of the former group (Aspidobranchiata and Ctenobranchiata) seem to have existed in those early times, but Pteropoda are the only Euthyneuran types known. These forms ("sea-moths") are abundant in recent plankton, but are mostly ill-suited for preservation as fossils. It is possible that the Lower Palaeozoic Pteropods may represent a truly primitive stock, from which not only Gastropods, but even Cephalopods, may have sprung, while modern sea-moths perpetuate the early forms with much reduction of shell-substance. *Hyolithes*, which ranged throughout the Palaeozoic, was sufficiently abundant to be almost a rock-former in parts of the Cambrian. There is little distinctive in its tubular shell, but specimens have been found in Middle Cambrian shales of British Columbia which, by preservation of the soft-tissues, confirm belief in the Pteropod affinities of the genus. Another group of possible Pteropods was that illustrated by *Tentaculites* (extraordinarily abundant in the Ordovician (Pl. x. fig. 4), and surviving to the Devonian) and *Conularia* (Ordovician to Jurassic, least rare in the Silurian). The latter type had a partly septate shell with roughly quadrangular section.

Aspidobranchiate Streptoneura were essentially Palaeo-

zoic forms, although such types as *Patella* and *Trochus* are common at the present day. One of the simplest of the group was *Bellerophon*, a coiled shell resembling that of a Nautiloid in shape. It was not uncommon in the Ordovician and Silurian, but became more important in the Upper Palaeozoic. The long-lived genus *Pleurotomaria* appeared first in the Silurian, but its acme was in the Mesozoic. *Murchisonia* and *Euomphalus* are two genera that originated in the Lower Palaeozoic (the former perhaps in the Cambrian), but were better developed in the Carboniferous. *Platyschisma* and *Omphalotrochus* (Pl. x. fig. 3) both survived to the last-named period; they were abundant in the Middle and Upper Silurian.

The Ctenobranchiate section is divided into five superfamilies on radular characters. Three of these groups seem to have been present in the Lower Palaeozoic, but it is impossible to be certain of the systematic position of many genera. Gymnoglossa, which are apparently degenerate in structure and habits, may have been represented by *Macrocheilus* and *Loxonema* in the Silurian, but these genera were both more abundant in the Carboniferous. The multidentate Ptenoglossa, a small group of usually rare forms, seem to include *Holopella*, which is fairly common in the Silurian, particularly in the Kirkby Moor Flags of Westmorland. The Taenioglossa, the largest series of later Gastropods, showed possible members of the Littorinidae in the Ordovician, and somewhat problematical Capulidae in the Cambrian (*Capulus* and *Stenotheca*) and Silurian (*Platyceras*). These three genera were mainly Palaeozoic, but *Capulus* is still extant.

Cephalopoda were far from rare in the Lower Palaeozoic, but known forms seem restricted to the Nautiloid branch of Tetrabranchiata. The living genus *Nautilus* is the sole survivor of an extensive series of

Cephalopods which appeared in the Ordovician, reached its acme in the Palaeozoic, and has lingered with undistinguished persistence since the Permian. It is interesting to note that this group of Tetrabranchs, the earliest to arise, is still living; while the Ammonoids, whose differentiation was deferred until the Devonian, are utterly extinct. No types referable to Dibranchiata (the only successful modern Cephalopods) are known from the Palaeozoic. The most abundant Nautiloids of the Ordovician and Silurian are "Orthoceracones" —straight, tubular shells with saucer-shaped septa. *Orthoceras* (Pl. x. fig. v.) is rare in the Ordovician, as, indeed, are most other genera; but, with its ornamented relative *Dawsonoceras*, it is profusely distributed in the Silurian. In the Ludlow series remarkable, probably phylogerontic, forms allied to *Gomphoceras* are not uncommon. "Cyrtoceracones," resembling bent *Orthoceras*-forms, were represented by the Silurian *Ascoceras*, while *Ophidioceras* and *Lituities* showed some degree of enrolment preparatory to the "Nautilicone" condition. Definitely "*Nautilus*"-like forms seem not to have been developed before the Devonian.

(K) ARTHROPODA

With the probable exception of Protozoa, Arthropods are by far the most abundant Invertebrates of the present period. Marine and lacustrine plankton teems with small Crustacea, while larger aquatic forms abound in deep and coastal waters. On land and in the air insects and arachnids, for all their normally small size, can make other life miserable and precarious by their insistent habits, although they excite wonder by the intricacy and beauty of their structures. Most Arthropods secrete "shells" of chitin, but in marine forms a fair

proportion of lime-salts is added. Although chitin is a remarkably resistant substance, the usual delicacy of Arthropod coverings and the loosely segmented quality of many types, make their satisfactory preservation rare. The normal mode of growth by ecdysis, while providing a succession of envelopes from each individual, results in production of much fragmentary material. A more or less argillaceous tomb is necessary for prolonged preservation; but with such a matrix there is no limit to the duration of chitin.

From evidence available, there seems justification for belief that Arthropods have been relatively as abundant in all recorded periods of the past as they are to-day. In the Palaeozoic era Trilobites seem to have more than filled the position occupied by Crabs and Lobsters at the present time; while small Ostracoda are scattered through suitable matrices with equal profusion in the Ordovician and Cretaceous. Insects are ill-adapted for fossilization; the considerable numbers known, even from the Carboniferous, are suggestive of their existence in vast swarms. It is a striking fact that the number and variety of large Arthropods known from the Palaeozoic are much in excess of those of later faunas. With few exceptions Cambrian forms were Crustacea; all Lower Palaeozoic types were Branchiata. Myriopods and Insects are unknown before the Devonian.

Trilobites are among the most familiar fossils of the Palaeozoic. In spite of their apparent complexity, these extinct Crustaceans were among the simplest forms of the phylum. The long succession of separate, similarly specialized segments that characterized most Cambrian types can be compared with the simple repetition of parts in a caterpillar. In most Trilobite lineages there appears a progressive tendency towards incorporation of more segments into the pygidium (see Pl. viii. fig. 4)—

the cephalon never seems to comprise more, or less, than five.

Of the three orders usually recognized among Trilobites, two (Hypoparia and Opisthoparia) were well developed at the lowest horizons of the Cambrian. They reached well-defined acmes in the Ordovician, when many new families originated before the earlier ones had disappeared. The Proparia arose in full differentiation in that period. During the Silurian Trilobites continued to show specific abundance, but a marked decline in families set in. This became more marked in the Devonian, after which a few gerontic types lingered to the end of the Palaeozoic.

The Hypoparia were represented in the Cambrian by two families only, both of which were virtually restricted to that period. The minute, almost "larval," *Agnostus*-series, with but two body-segments and elusively similar cephalia and pygidia, are locally abundant in the Middle and Upper Cambrian of Wales; the group ranged from the Lowest Cambrian to the Lower Ordovician. A somewhat different series of Hypoparians arose in the latter period, comprising larger and curiously specialized types of which *Trinucleus* (Pl. x. fig. 8) and *Ampyx* are the best-known examples.

Opisthoparia were the most abundant and varied of Lower Palaeozoic Trilobites. No fewer than eleven families occurred in the Cambrian; of these three were absolutely restricted to that stage, and the remainder disappeared in the succeeding period. In the absence of Graptolites, Trilobites prove well adapted for zonal subdivision of the Cambrian. The spinous Mesonacidae, with large cephalia, numerous thoracic segments, and minute pygidia, characterize the Lower Cambrian (*Olenellus* stage). Nearly allied Paradoxidae, often attaining very great size, are restricted to the Middle Cambrian

(*Paradoxides* stage); and more advanced Olenidae, with smaller cephalae and more extensive pygidia, are abundant in the Upper Cambrian (*Olenus* stage), though ranging throughout the period and into the Ordovician. *Olenus*, *Parabolinella* (Pl. x. fig. 6) and *Angelina* (Pl. iii. fig. 3) are the best known British genera of the family. *Sao*, a Cambrian Olenid, is remarkable for the relatively complete knowledge available of its post-larval ontogeny; *Triarthrus*, an Ordovician genus, is even more noteworthy on account of discovery of specimens with perfectly preserved appendages. In the Ordovician the families Asaphidae and Illaenidae were perhaps the most important. *Asaphus* and *Ogygiocaris* (Pl. x. fig. 7) are abundant in the Llandeilo stage, and by their large size and multiple pygidia seem to represent late forms in their particular lineages. *Aeglina* is a curious type from this period, with compound eyes rivalling those of many Hymenoptera in size and complexity. It was probably adapted for life in the shadows of deep water. In the Silurian period the chief Opisthoparian families were the Proëtidae (which survived to the Permian), Lichadidae and Odontopleuridae. The grotesque, spinous character of the *Lichas*-series, and the "hedgehog" qualities of *Ceratocephala* and *Acidaspis*, were clearly phylogerontic features.

The Proparia were a small group of Trilobites (chiefly Ordovician and Silurian) that often attained extraordinary abundance. The four families usually recognized were all differentiated in the Ordovician, but became much more fully represented in the following period. *Encrinurus* is not uncommon in the Llandovery beds, and persisted to the Wenlock. The Calymenidae were a somewhat static group. Ordovician species of *Calymene* were very much like the famous "Dudley Locusts" of Wenlock age; while *Brongniartella* from

the Caradocian is closely comparable with *Trimerus* and *Homalonotus* of the Upper Silurian and Devonian. The Cheiruridae included the most bizarre types of Trilobites. *Cheirurus* itself had a disproportionately wide glabella, while *Sphaerexochus* and *Staurocephalus* had that feature inflated to a grotesque degree. Perhaps the most extraordinary member of the group was the Silurian *Deiphon*, in which the carapace was reduced to mere "scaffolding," except for the glabella, which formed a bulbous and warty protuberance. The Phacopidae, with compound eyes comparable with, but inferior in size to, those of *Aeglina*, were a family hardly less important than the Calymenidae. Large, relatively smooth forms of *Dalmanitina* are fairly common in the Caradocian, while *Phacopidella* and *Dalmanites* are abundant in Wenlock and Ludlow beds. All of these families, except the Encrinuridae, persisted into the Devonian, but the Phacopidae were the only abundant Proparia of that period.

Among true Crustacea, the four great groups of Branchiopoda, Ostracoda, Cirripedia and Malacostraca have representatives in the Lower Palaeozoic. The Branchiopods, surviving at the present day in the well-known *Apus*, are probably the most primitive Crustacea discovered, and are believed to be ancestral to all other members of the class. The delicacy of their chitinous coverings makes them uncommon as fossils, but it is interesting to note that *Protocaris*, a genus closely resembling *Apus*, occurred in the Lower Cambrian. The small bivalved Ostracoda are often abundant. Their first occurrence was in the Ordovician, and such types as *Leperditia*, *Beyrichia* and *Entomis* may be found thickly scattered in shales of Caradoc and Silurian age. Cirripedes (Barnacles) of Lower Palaeozoic date are rare and unsatisfactory. There is much uncertainty

as to whether certain small fossils are detached Cirripede plates or primitive Pelecypod shells. The curious, fir-cone-like *Turrilepas* is known from the Cambrian onwards, and seems to have disappeared in Devonian times.

Lower Palaeozoic Malacostraca all belonged to the primitive series Phyllocarida, usually showing superficial resemblance to "shrimps." *Hymenocaris* from the Cambrian, and *Ceratiocaris* (Pl. x. fig. 9) from the two succeeding periods, are the best known British representatives of the group.

Arachnids of the era belonged to the orders Synxiphosura, Eurypterida and Scorpionida. The first-named group was restricted to the Lower Palaeozoic, and included Trilobite-like forms that were probably ancestral to the *Limulus*-series and Eurypterids. That order is known from the Palaeozoic only, but ranged from the Cambrian to the Permian, with a marked acme in Silurian and Devonian times. *Beltina*, a problematical Eurypterid from the pre-Cambrian, is of doubtful systematic position. The two most familiar members of the order are *Eurypterus* and *Pterygotus*. The former genus lingered to the Permian, but was most prominent in the Upper Silurian. The classic locality for its occurrence is in the Isle of Oesel, whence specimens have been obtained from the fine Silurian marls in such perfect preservation that they can be detached from their matrix and mounted for microscopic study like recent material. *Pterygotus*, a gigantic form with peculiar outward similarity to certain contemporary Antiarchi (e.g. *Pterichthys*), appeared with *Eurypterus* in the Ordovician, but is best known in Britain from the Old Red Sandstone. Scorpions are found in the Upper Silurian of Scotland and elsewhere; they belong to a distinct family, and their order was not fully differentiated until the Carboniferous period.

CHAPTER III

UPPER PALAEOZOIC FAUNAS (PLS. XI. AND XII.)

(A) GENERAL ACCOUNT

THE products of almost all conditions of sedimentation are to be found among British Upper Palaeozoic strata. Some parts of the Old Red Sandstone, and certain sandstones and marls of the Permian, seem to have accumulated on land as mountain screes or desert dunes. Other local portions of the Old Red Sandstone give evidence of transitory lacustrine surroundings, while much of the Upper, and parts of the Lower, Carboniferous series were deposited in fresh water, meandering through delta-swamps. Broad tidal sand-flats of Mid-Carboniferous date produced the Millstone Grit, while shales and coral-reefs indicate different littoral conditions at lower horizons. The Permian Magnesian Limestone was formed in a gulf probably comparable with the Red Sea. Much of the Carboniferous Limestone appears to have developed on the floor of an open, but not deep, sea; the Radiolarian cherts of the Devonshire Culm suggests deposition in abysmal depths.

Great as is the variety of matrix, the selection of diverse faunal assemblages is somewhat limited. Terrestrial deposits are, on the whole, sadly unfossiliferous, and even the Coal Measures, with their wealth of plant-remains, enclose but few relics of Invertebrates. The Magnesian Limestone may have lost some proportion

of its included fossils during dolomitization; but the enclosed and "unhealthy" quality of the sea in which it was formed doubtless limited the numbers, as it dwarfed the individuals, of the indigenous fauna. Further, the bulk of British Devonian rocks (restricted in outcrop to Devonshire and Cornwall) has been caught in the toils of post-Carboniferous earth-movement and igneous activity, and is in consequence stratigraphically complex and lithologically obscure. The only Upper Palaeozoic series that is adequately fossiliferous (for Invertebrates) in Britain is the Lower Carboniferous. Many of the shales and limestones of that age compensate, by the abundance and good preservation of their faunas, for the unsatisfactory nature of palaeontological evidence at the other horizons.

The upheaval that brought the Silurian period to a close in the Downtonian stage resulted in development of an extensive area of land covering (with the exception of local and probably temporary lakes) all of the British area north of the "Mendip axis." In the hollows of this land-surface, the boulder-beds and desert-marls of the Old Red Sandstone were mingled with the products of contemporary volcanic eruptions. In the littoral belt of sea bordering the continent, detrital deposits accumulated in a lagoon whose southern boundary was, during part of the period, a fringing coral-reef. The Carboniferous period commenced with the breakdown of the "Mendip" shoreline, and consequent northward encroachment of the Devonian sea. Before this tendency was checked, most of England and Ireland (save for local islands of which "Wales" was the chief) became submerged, and the Carboniferous Limestone was accumulated. Towards the Cheviots the purity of the sea-water declined, under influence of the surviving "highlands"

and only occasional inroads of marine conditions reached the Midlothian "lake-basin." However, proximity of the sea induced climatic changes there; the "Coal-Measure" conditions of the Calcareous Sandstone stage are in marked contrast to the desert features shown by the Upper Old Red Sandstone. Meanwhile, the "Devonshire" area seems to have undergone varied and violent changes of level, resulting in the complex rock-series of the Culm Measures, which contain Radiolarian cherts indicative of deep water, and Anthracitic material suggestive of almost terrestrial conditions.

The brief success of the Carboniferous Limestone sea in invading "Lake Caledonia" was followed by diversion of a vast amount of sediment on to the British area. Sand-banks and mud-flats began to spread southwards from the Cheviots, silting up the sea-basin and smothering islands that had defied the sea itself. Gradually these deposits produced a delta, from whose marshy flats marine conditions were eventually excluded. Marine bands, often crowded with fossils, occur in the Lower Coal Measures, but such intercalations are rare in the main parts of the coal-bearing strata.

A fresh paroxysm of upheaval, the "Pennine Uplift," began to affect the British area before the end of the Coal Measures, and continued more or less persistently throughout the Permian. On the western side of the Pennine chain, topography reminiscent of parts of the Old Red Sandstone land-area was produced, resulting in lacustrine marls and "brockrams" fallen from fault-scarps or volcanic peaks. The vast plutonic intrusions of Devonshire and Cornwall belong to this episode; their development mutilated and metamorphosed all earlier rock-systems of that district. On the eastern side a synclinal depression (complementary to the Pennine anticline) let in a gulf of the sea in North-

Eastern England, but the Magnesian Limestone therein deposited gives but feeble indication of the important marine deposits of the European and Asiatic Permian. Before the end of the period, the gulf was silted up, and almost the whole of the British area was brought under the desolate monotony of the Triassic desert.

Although many of the groups of organisms dominant in Lower Palaeozoic times persisted through these later periods, there is a marked difference in the general faunas of the two eras. Graptolites have become extinct (for all practical purposes); Brachiopods, though still abundant, are represented by acmaic stages of quite different groups from those successful in the preceding era; while Trilobites have lost much of their earlier prominence. If four types are to be selected as particularly important in Upper Palaeozoic times, the choice would undoubtedly fall on Tetracorals, Camerate Crinoids, Productid and Spiriferid Brachiopods, and "Goniatite" Cephalopods. Many groups of Arthropods are more fully known from the Carboniferous than from any other horizons; but the special nature of their occurrence in the Coal Measures makes comparison with previous or later faunas impracticable.

(B) PROTOZOA

The Protozoa are more fully represented in the Upper Palaeozoic than in older periods. Foraminifera and Radiolaria both play the part of rock-formers in the Carboniferous series; the "Radiolarian Culm" of Devonshire is one of the richest stores of these small fossils at any horizon in British strata. In the North of England, important masses of the Carboniferous Limestone are built of Foraminifera. It is a point of interest that in both cases the respective orders include many

species of such size that they can be readily seen with the naked eye, and may even be separated from the matrix.

Devonian Foraminifera are hardly superior to those of the Silurian in abundance or variety; and, in view of the obscure condition of British strata of this type, can be ignored. But in Carboniferous times the order rose to a position of faunal importance. Plentiful development of more or less open-sea limestones may account, in some measure, for the abundance of Foraminifera, but evolutionary progress in the secretion of durable tests is probably a contributory cause. Nowhere in Britain do the Carboniferous strata show the characters of Foraminiferal ooze, but the less pure parts of the Mountain Limestone of Northern counties are locally rich in the "arenaceous" form *Saccamina*. A comparable part is played by *Fusulina* (a member of the *Nummulite* family) in Upper Carboniferous Limestones in Eastern Europe. The long-lived group of the Textulariidae is well represented, especially by forms with "agglutinating" habit. Permian Foraminifera correspond very closely with those of the preceding period, but they are naturally very scarce in Britain.

Among Radiolaria, the Spumellaria still predominated in the Upper Palaeozoic; the more complex Nassellaria occur in relatively small, though far from negligible, numbers.

(C) PORIFERA

Important additions to the Porifera were initiated in the Upper Palaeozoic. All the types found in the older series continued (Receptaculitidae disappearing in the Carboniferous), while siliceous Tetractinellids, and the Calcispongiae, made their first appearance. With the exception of the Hexactinellid *Hyalostelia*, sponges are usually rare in British Devonian and Carboniferous rocks.

(D) COELENTERATA

The Devonian and Carboniferous periods included reef-building episodes in Britain, but the Permian deposits are unsuited for development or preservation of Coelenterates. Tetracoralla and Tabulata were still the predominant "Corals," but the former series tended to outweigh the latter in importance, particularly in the Carboniferous. The well-known Devonian "marbles" of South Devonshire are largely built of Favositids, Cyathophyllids and *Heliolites*.

The most abundant genera of Devonian Tetracorals are *Cyathophyllum*, *Acervularia*, *Phillipsastraea* and *Calceola* (Pl. xi. fig. 1). Their facies is perhaps more reminiscent of the Silurian than predicative of the Carboniferous. The latter period is, as regards the lower (marine) portions, zoned by evidence based chiefly on Tetracorals. Relatively simple Zaphrentids characterize the lower horizons of the Carboniferous Limestone, while more elaborate Cyathophyllids, such as *Lonsdaleia* and *Lithostrotion* (Pl. xi. fig. 2), prevail at higher levels. Apart from a few possible Mesozoic and Recent members of the group, the Carboniferous Tetracoralla were the last of their kind.

The "Perforate" section of the Hexacoralla is sparingly represented in the Upper Palaeozoic by the family Eupsammiidae (which arose in the Silurian and persists at the present day).

The Alcyonarian genus *Heliolites*, which attained considerable importance in Silurian reefs, maintained its position in the Devonian, but is unknown from the Carboniferous.

Devonian Tabulata are familiar objects in polished slabs of limestone, the Favositid genera *Pachypora* and *Alveolites* predominating. The small and peculiar form

known as *Pleurodictyum* (occurring as casts including an apparently symbiotic worm) is a well-known Middle Devonian fossil; the genus lingered into the Lower Carboniferous, in which stage the massive, honeycomb-like colonies of *Michelinia* were the most effective representatives of the family. *Syringopora*, a form similar to the recent *Tubipora* in habit, is locally abundant in the Lower Carboniferous; while *Chaetetes*, the only Tabulate to survive beyond the Palaeozoic, sometimes builds massive sheets of limestone.

Among Hydrozoa, the Stromatoporoidea were of first importance in Devonian reef-limestones, but suffered extinction in the Carboniferous. Dendroid Graptolites, which may either be persistent types or reversionary mimics of early forms, are to be found, though rarely, in the Devonian and Carboniferous; while the essentially Silurian genus *Monograptus* has been recorded from the Devonian. Sporadic discoveries of such a nature fail to detract from the value of the Graptolites as indices of Lower Palaeozoic horizons.

(E) ECHINODERMATA

In respect of Echinodermata, the Upper Palaeozoic could be described as the "age of Blastoids, Camerate Crinoids and Perischoechinoids." These types all had representatives in the Silurian, but none survived the Permian. The extreme scarcity of Echinoderms in the last Palaeozoic period is somewhat mysterious, but it helps to emphasize the contrast between Carboniferous and Mesozoic types.

Late forms of Rhombiferan Cystids, and perhaps of Amphoridea, have been recorded from the Devonian, but they are inconspicuous—comparable with surviving Graptolites in stratigraphical insignificance. Minute, scaly

Edrioasteroids, usually cemented by the aboral surface, perpetuated the class (or order) beyond the Devonian. *Agelacrinus* is typically Devonian, and *Lepidodiscus* has been found in the British Lower Carboniferous.

Blastoids were pre-eminently Devono-Carboniferous forms. Like other recognizable fossils, they are rare in the British Devonian, but *Orbitremites* (Pl. xi. fig. 3) and *Phaenoschisma* may be found in local "nests" in parts of the Carboniferous Limestone. The Bolland district of Lancashire is most prolific in these small forms. The Devonian *Nucleocrinus* is a precursor of the former genus; *Pentremites*, from the American Sub-Carboniferous (showing "petaloid" ambulacra and elaborate hydrospires), is more nearly related to the latter. The last known Blastoid died in early Permian times.

Inadunate Monocyclic Crinoids persisted in their unaspiring course. *Symbathocrinus* is not uncommon in the Carboniferous Limestone. Both Adunata and Camerata failed to survive the Carboniferous period, but in their short careers attained great abundance. *Hexacrinus* is a well-known Devonian Adunate; *Platycrinus* (Pl. xi. fig. 4) is one of the commonest Crinoids of the Carboniferous Limestone. *Acrocrinus*, one of the latest Adunata, is remarkable for inclusion of numerous accessory plates between the basal and radial circlets, giving a spurious "Camerate" appearance to the calyx. True Monocyclic Camerata were the chief rock-formers among Echinoderms. They attained their acme, and reached extinction, in the Carboniferous. *Melocrinus* is a familiar Devonian type on the Continent, but from the British standpoint *Actinocrinus* and *Amphoracrinus* (exclusively Carboniferous genera) are the most important. Columnals of these forms constitute much of the Carboniferous Limestone (Pl. i. fig. 2), and their massive, tegminate crowns are locally abundant and well-preserved.

Dicyclic Crinoids, in spite of their longer range and later specialization, show comparable diversity in the Upper Palaeozoic. Inadunata are especially abundant. *Cupressocrinus*, with simple, curiously massive, arms, is one of the most characteristic Devonian Crinoids. *Cyathocrinus* survived from the Silurian; while *Poteriocrinus*, *Graphiocrinus* and *Woodocrinus* represented in the Carboniferous the most prolific suborder (Dendrocrinoida) of the Mesozoic. Flexibilia were not yet abundant, but the small *Mespilocrinus* occurs in the Carboniferous Limestone. Dicyclic Camerates are few, but such as they are correspond with their Monocyclic equivalents in range. *Rhodocrinus* and *Gilbertocrinus* are the most familiar Carboniferous genera. The latter is remarkable in possessing hollow, branched extensions, of unknown function, from the tegmen, between which arise the slender, pinnulate arms.

The only noteworthy feature in the scanty Holothurian fauna of the Upper Palaeozoic is the occurrence of true Synaptidae (indicated by characteristic "wheel" spicules) in the Permian. Stelleroids are not much more satisfactory than those of the earlier era. Bundenbach is a classic locality for Devonian forms, which occur as petrifications in pyrites, readily cleared from the surrounding slate. *Onychaster* is a curious Ophiuroid from the Carboniferous.

Upper Palaeozoic Echinoidea belong to the peculiar group sometimes called "Perischoechinoidea." Unlike all later types, they have more than two columns of interambulacral plates, and many possess extreme ambulacral multiplicity. The tests were commonly ellipsoidal in form; and the coronal plates, though often massive, were imbricate in arrangement, giving flexibility comparable with that shown by the aberrant Echinothuriidae of later times. Two main trends of morpho-

geny can be traced among Perischoechinoids. In the one (illustrated by *Lepidocentrus* in the Devonian, and by *Perischodomus*, *Palaeochinus* and *Archaeocidaris* in the Carboniferous) the interambulacra became multicolumnar (often with unituberculate plates), while the ambulacra retained two columns with little or no modification. The last-named genus seems to have given rise to the Cidaroid stock (whence sprang all Euechinoids) through *Eocidaris* and *Miocidaris* in the Permo-Trias. The other direction of evolution (represented by *Melonechinus* (Pl. xi. fig. 5) and culminating in *Lepidesthes*) admitted some degree of complexity into the interambulacra, but specialized in multiplication of ambulacral columns. These large, scaly types hardly survived the Carboniferous period. The anomalous and energetic elaboration of Upper Palaeozoic Echinoids may be regarded as an expression of phyloneanic specialization. Out of a welter of unsuccessful experiments, the efficient Cidaroid stock emerged during Permian times.

(F) POLYZOA

The Polyzoan fauna of the Upper Palaeozoic is relatively meagre. All of the orders present in lower strata persisted until the Permian, but the two of chief importance, Trepostomata and Cryptostomata, became extinct in that period. The "Monticuliporoidea" were less abundant than in the Silurian, but the Cryptostomatous Fenestellidae were dominant forms. *Fenestella* occurs in widespread clusters in the Carboniferous Limestone (particularly in North Wales and the Isle of Man), and assumes almost rock-forming qualities in the Magnesian Limestone of North-Eastern England. Cyclostomata are generally scarce, the only group of importance being the Fistuliporidae. Ctenostomata

pursued their quiet and inconspicuous course, while Cheilostomata were not yet differentiated.

(G) BRACHIOPODA

In spite of the rapidly increasing elaboration of other phyla (particularly Mollusca), the Brachiopoda maintained a position of first importance in the Upper Palaeozoic. The virtual disappearance of the Atremata and Neotremata was fully compensated by the acmaic exuberance of the Productidae among Protremata, and the maintained prominence of Spiriferacea, with awakening specialization of Rhynchonellacea, among Telotremata. In the Devonian and Carboniferous periods, Brachiopods still counted as local rock-formers, and they are among the most abundant members of the exiguous British Permian fauna.

The only group of Atremata to survive the Silurian was the late stock of the Lingulidae. *Lingula* occurs with some frequency in the Devonian, and is there accompanied by a few other genera. But in the Carboniferous the family declined towards that humble condition in which it still exists.

The record of the Neotremata is similar. Discinacea persisted in some variety into the Devonian, but became so reduced in Carboniferous times that *Orbiculoidea* (Pl. iv. fig. 1) was almost their sole representative. Craniacea are not unknown from the Upper Palaeozoic, but deserve no more flattering mention.

Among Protremata, the prolific stock of the Orthacea met its doom in the Permian. While typical genera (such as *Dalmanella*) remained in the Devonian, the majority of Carboniferous forms were clearly phylogerontic. *Schizophoria*, with its spinose surface, and *Enteletes* with elaborate ornament, illustrate late phases in Orthid evolution. The Strophomenacea, though

still surviving, also collapsed in Permian times. *Leptaena* occurs in the Lower Carboniferous with characters hardly altered from those of Silurian species, while other types of that group (e.g. *Davidsonia*) assumed the "Neotrematous" habit of complete sessility with atrophy of the pedicle. *Orthotetes*, an ally of *Strophomena* which is not uncommon in the Carboniferous Limestone, shows similar tendencies. The first members of the surviving group of Thecidiidae made their appearance in the Carboniferous, and were usually much larger than their descendants. The family Productidae far excels in importance all other Upper Palaeozoic Protremata. *Chonetes*, its simplest expression, ranges from the Silurian to the Permian. True Productids appeared in the Devonian, and are almost the commonest of Carboniferous marine fossils. Profuse development of spines, attainment of gigantic proportions, and progressive loss of pedicle-function show that *Productus* (Pl. xi. fig. 6) is, in some ways, a phylogerontic stock among Protremata. Cementation, either by spinous outgrowths or actual "Neotrematous" adhesion, became more and more typical as the group passed through the Carboniferous to the Permian; it culminated in the extraordinary *Hippurites*-like *Richthofenia* of the latter period. Pentameracea lingered through the Upper Palaeozoic, being represented by such small and specialized types as *Camarophoria* in the Carboniferous and Permian. In that period they disappeared.

Telotre mata showed well-defined members of all three sections in the Devonian. The Rhynchonellids had increased far beyond their Silurian quality, *Pugnax* (Pl. xi. fig. 7), *Hypothyridina* and *Allorhynchus* being particularly abundant in the Carboniferous Limestone. Terebratulacea with short loops appeared for the first time in the Devonian. These Terebratuloida branched

out into three families, two of which (and an important part of the third) are restricted to the Upper Palaeozoic. *Centronella*, *Stringocephalus*, *Megalanteris* and *Dielasma* (Pl. xi. fig. 8) represent these early, short-lived experiments of the series. True "Terebratulas" are unknown before the Trias. Among the Spiriferacea, the best known and most fully specialized representatives are of Devonian and Carboniferous age. The Atrypidae lingered into the Devonian, but were overshadowed by the Spiriferidae. *Spirifer* (Pl. xi. fig. 9) itself (in the broad sense of the term) is scarcely less common in the Carboniferous Limestone than *Productus*, and attained peculiar proportions in such sections as *Syringothyris*. The Suessiidae, which survived into the Jurassic, are rarely abundant, and the Meristellidae dwindled to extinction in the Devonian. Two new families arose in that period. The anomalous Uncitidae, with dorso-lateral pouches and rostrate form, are typically Devonian, but persisted to the Permian; while the superficially simple but inwardly complex Athyridae are among the most characteristic Upper Palaeozoic Brachiopods. *Athyris* is locally abundant in the Carboniferous Limestone; its aberrant, often cemented, descendants reached their phase of gerontic acceleration in the Trias.

(H) MOLLUSCA

Upper Palaeozoic Mollusca show a marked increase in numbers and variety upon the exiguous fauna of the preceding era. Opportunities for discovery of terrestrial and fresh-water types have but slight influence on this quality. Many genera and families of Pelecypods that arose in the Silurian reached their acmes in the Carboniferous, while an even greater number of fresh types appeared. Gastropods maintained their previous qualities, but showed small tendencies to differentiation

of new forms. The most noteworthy advance was the appearance of Tectibranchiate and Pulmonate Euthyneura. Cephalopods were chiefly responsible for the importance of the Upper Palaeozoic Molluscan fauna. Nautiloids were in an acmaic stage during the Devonian, and remained abundant in the Carboniferous; while Ammonoids arose in the former period and were approaching their transcendent acme in the Permian. It is unfortunate that conditions were unsuitable for successful life or fossilization of Mollusca in the British area except in the Carboniferous.

Prionodesmacea were still the most important, though not the only, Pelecypoda of the Upper Palaeozoic. Palaeoconcha were better developed in the Carboniferous than at any other period; *Sanguinolites* and *Cardiomorpha* are two familiar types. Among Taxodonts *Nuculana* and *Leda* are often abundant, especially in the Lower Carboniferous of Scotland; while *Paralledon*, a form which, with its descendants, was important in Mesozoic and Cainozoic faunas, appeared in the Devonian. Schizodonts were the most prolific Upper Palaeozoic bivalves. *Conocardium*, a curious and somewhat problematical type, is found in the Carboniferous Limestone. The Pteriidae were abundantly represented. *Pteria* and *Pseudomonotis* appeared in the Devonian, but both genera are more characteristic of Mesozoic horizons. *Posidonomya* (Pl. xii. fig. 1) is an important fossil of the Lower Carboniferous. The Pernidae, destined to rise to great prominence in the Mesozoic, had their origin in the little *Bakewellia* of the Permian. True Ostreidae occur in the Carboniferous, and *Schizodus* initiated (in the Permian) the essentially Mesozoic family of the Trigoniidae. One of the most characteristic series of Upper Palaeozoic Schizodonts were the Cardiniidae. *Naiadites* and *Carbonicola* occur in swarms in some

(probably brackish) horizons in the Coal Measures, while *Archanodon* from the Old Red Sandstone (doubtfully placed in this group) is the oldest known freshwater Pelecypod. Isodonta began to show some progress in Carboniferous times; both of the common stocks, *Pecten* and *Lima*, date from that period. But the most important member of the series is *Pterineopecten* (Pl. xii. fig. 2), one of the commonest fossils of marine bands in the Lower Coal Measures. *Modiolus*, a living genus of Dysodonts, appeared in the Devonian, while the rock-boring *Lithophagus* has been recorded from the Carboniferous. The only Palaeozoic family of Anomalodesmacea (Pholadellidae) is represented by *Allorisma*, a mussel-shaped shell not uncommon in the Carboniferous, but rare in the Permian. Records of Teleodesmacea from the Upper Palaeozoic are doubtful, but *Pleurophorus*, if rightly placed in this order, gave it abundant representation in the Permian. The degenerate, burrowing types of *Pholas* and *Teredo* are said to occur in the Carboniferous, but quite different animals might have produced the crypts ascribed to them.

Aspidobranchiate Streptoneura retained their prominence among Upper Palaeozoic Gastropods. Many of the genera that occurred in the Silurian, such as *Bellerophon* (Pl. xii. fig. 4), *Murchisonia* and *Euomphalus*, survived into the later era with equal, or greater, numbers. The Euomphalidae are particularly characteristic of the Carboniferous Limestone, *Euomphalus* (Pl. xii. fig. 3), *Schizostoma*, *Straparollus* and *Platyschisma* being familiar genera. The small, limpet-like Fissurellidae made their appearance at that horizon; *Naticopsis* was perhaps a precursor of the common Neritidae of to-day. Among Ctenobranchiate types few innovations were made at this stage. Gymnoglossa were still represented by *Macrocheilus*, and especially by *Loxonema*;

PLATE XI

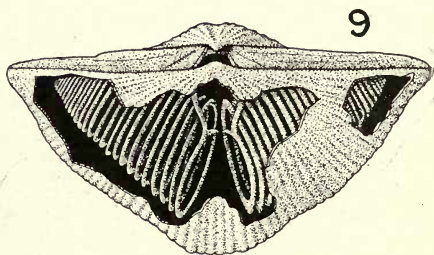
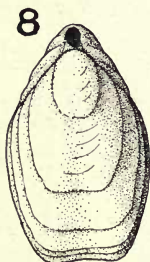
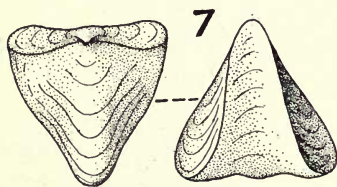
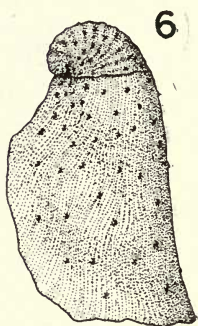
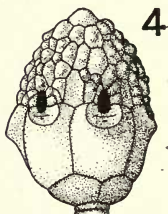
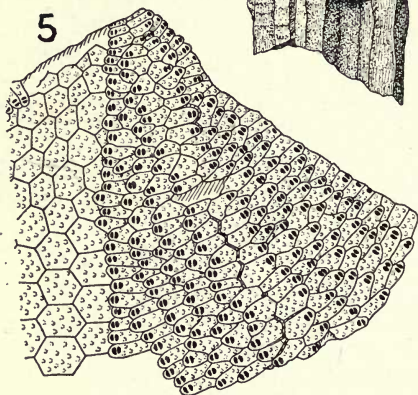
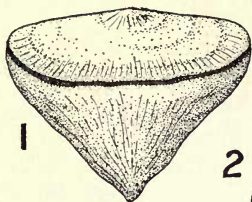




PLATE XI

UPPER PALAEOZOIC FOSSILS

- FIG. 1. *Calceola sandalina*. Middle Devonian, Gerolstein, Eifel.
- FIG. 2. *Lithostrotion basaltiforme*. Carboniferous Limestone. Poyll
Vaish, Isle of Man.
- FIG. 3. *Orbitremites ellipticus*. Carboniferous Limestone, Clitheroe.
- FIG. 4. *Platycrinus gigas*. Carboniferous Limestone, Clitheroe.
- FIG. 5. *Melonechinus keepingi*. Carboniferous Limestone. (Modified
from Jackson.)
- FIG. 6. *Productus semireticulatus martini*. Carboniferous Limestone,
Castleton, Derbyshire.
- FIG. 7. *Pugnax acuminatus*. Carboniferous Limestone, Dovedale.
- FIG. 8. *Dielasma hastata*. Carboniferous Limestone, Castleton.
- FIG. 9. *Spirifer striatus*. Carboniferous Limestone. (After Davidson.)

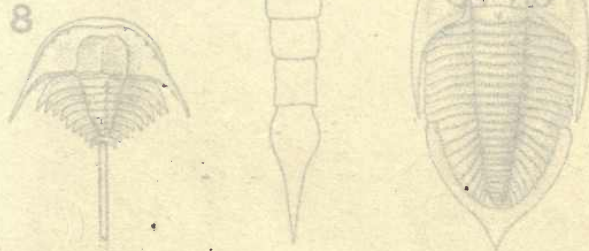


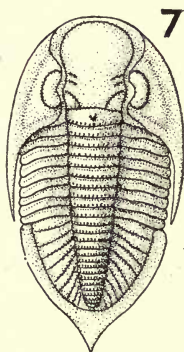
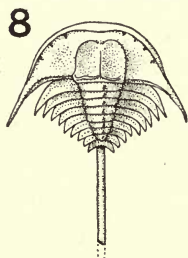
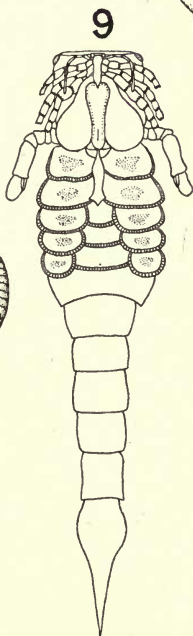
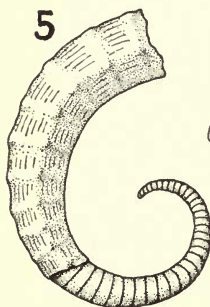
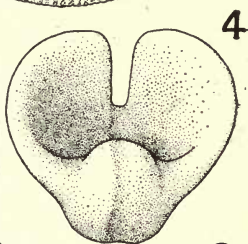
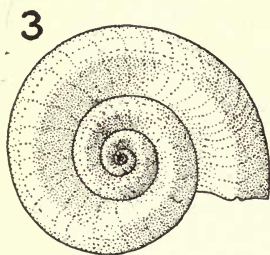
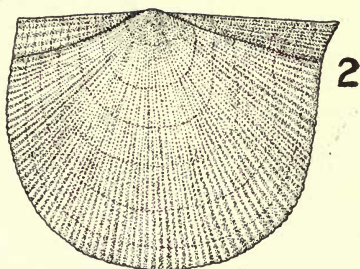
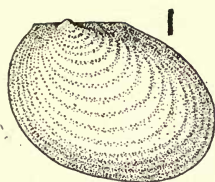


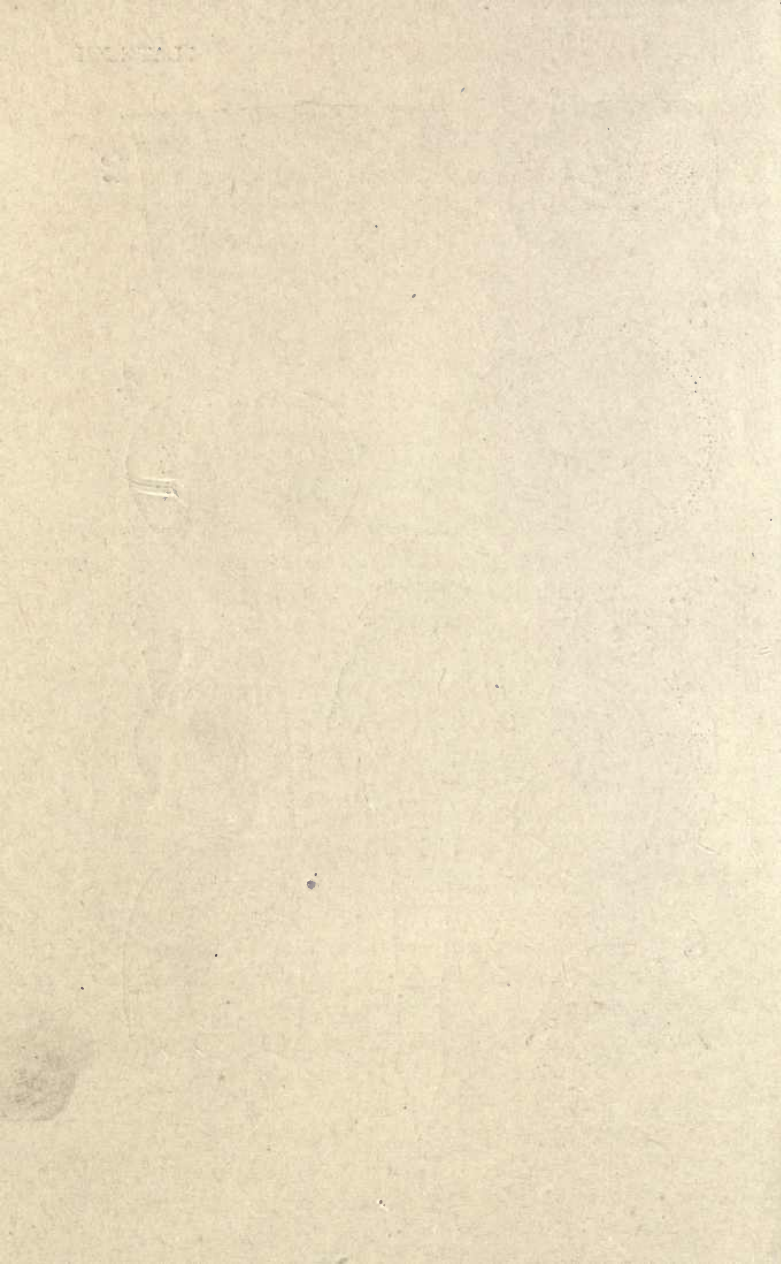
PLATE XII

UPPER PALAEOZOIC FOSSILS

- FIG. 1. *Posidonomya becheri*. Lower Coal Measures, near Sheffield.
- FIG. 2. *Pterineopecten papyraceus*. Lower Coal Measures, Stalybridge.
- FIG. 3. *Euomphalus pentangulatus*. Carboniferous Limestone, Castleton.
- FIG. 4. *Bellerophon* sp. Carboniferous Limestone, Kendal, Westmorland.
- FIG. 5. *Cyrtoceras nodosum*. Middle Devonian, Gerolstein.
- FIG. 6. *Glyphioceras crenistria*. Carboniferous Limestone, Poyll Vaish, Isle of Man.
- FIG. 7. *Phillipsia eichwaldi mucronata*. Carboniferous Limestone. (After Woodward.)
- FIG. 8. *Belinurus reginae*. Coal Measures. (After Woodward.)
- FIG. 9. *Slimonia acuminata*. Old Red Sandstone. (After Laurie.)







while *Capulus* and the *Serpula*-like *Vermicularia* foreshadowed the teeming *Taenioglossa* of later periods. The *Euthyneura* perhaps showed most evolutionary activity among Gastropods. Tectibranchiata, such as *Actaeonina*, appeared first in the Carboniferous; Conulariid Pteropods almost disappeared at the same stage; and the earliest known Pulmonate, *Hercynella*, occurred in the Devonian. The oldest recorded land-snail, *Dendropupa*, has been found in the Coal Measures.

Cephalopoda are striking, and often abundant, fossils in the Upper Palaeozoic. Nautiloids were joined by Ammonoids in the Devonian; the record of the former is one of slow decline, that of the latter of extraordinarily rapid specialization. *Orthoceras* maintained its primitive form, with morphogenetic monotony, throughout the era, and endured even to the Trias. *Cyrtoceras* (Pl. xii. fig. 5) is a characteristic Devonian Nautiloid; while more completely discoidal shells, such as those of *Stroboceras* and *Coelonautilus*, are relatively abundant in the Carboniferous. But few groups of Nautiloids survived the Palaeozoic; all such enduring types (except *Orthoceras*) were more or less strongly involute.

The Upper Palaeozoic has been described as the "age of Goniatices." Although later discoveries among Permian Ammonoids have shown this generalization to be inaccurate, the stage of evolution indicated by the comprehensive word "Goniaticite" was certainly prevalent in Devonian and Carboniferous times. *Bactrites*, a straight shell distinguished from *Orthoceras* (or its ally *Protobactrites*) merely by the ventrad situation of the siphuncle, may be the true radical of the Ammonoid stock. It is found in the Devonian in company with a large series of more advanced forms. Of these, the Clymeniidae are especially interesting. *Clymenia*, unlike all other Ammonoids, has the siphuncle on the dorsal side of

the shell-cavity. It is quite restricted to the Devonian (where, with its allies, it occurs in abundance), and probably represents an unsuccessful neanic experiment in the early evolution of the order. Typical "Goniatites," such as *Anarcestes*, *Tornoceras*, *Aganides* and *Gephyroceras*, are not uncommon in the Devonian, and often show strong involution and pronounced septal corrugation. The last-named genus is interesting, since it was probably directly ancestral to the familiar *Ceratites* stock of the Trias. The commonest Goniatites of the Carboniferous are *Prolecanites* and *Glyphioceras* (Pl. xii. fig. 6) (Lower and Upper Carboniferous Limestone respectively) and *Gastrioceras* (Coal Measures). In some parts of the British Carboniferous sequence the two last genera are almost rock-formers, *Gastrioceras* being particularly abundant in marine bands of the Lower Coal Measures, and supplying much of the calcareous matter that caused development of "bullions" and "coal-balls" in such seams. In the Permian, *Medlicottia* continued and amplified the qualities shown in *Prolecanites*; while *Popanoceras* represented a similar post-Goniatite stage, with complete involution and practically "Ammonite" sutures, in a different lineage. No Ammonoids have been found in the Magnesian Limestone; the unhealthy waters of the enclosed gulf in which that deposit was formed were evidently repugnant to robust types. No forms referable to Dibranchiate Cephalopods have yet been discovered in the Palaeozoic, although Belemnoids (probably modified from some Orthoceratid ancestor) were definitely established in the Trias.

(K) ARTHROPODA

The two Arthropod groups most characteristic of the Lower Palaeozoic (Trilobita and Eurypterida) persisted throughout the later periods, but showed rapid diminu-

tion in importance. Both disappeared completely in the Permian. The failure of these types was in large measure counterbalanced by the rise of Xiphosura and Scorpionida among Arachnids, and by the appearance of Myriopods and Insects. The swamp-conditions of Coal Measures gave unusual opportunities for preservation of the last two series; their absence from Lower Palaeozoic horizons may well be due to lack of evidence rather than to actual non-existence.

Hypoparian Trilobites were represented in the Devonian by the solitary genus *Harpes*, a form showing many affinities with the Trinucleidae of the Ordovician. *Harpes* comprises in a curious way features of over-specialization in the cephalon with reversionary (or retarded) tendencies in the pygidium. Opisthoparia maintained four families in the Devonian; these were reduced to three in the Carboniferous, and one (Proëtidae) in the Permian. *Goldius* (usually called *Brontes*), the genus that failed in the Devonian, shows clearly the gerontic quality of a large pygidium. The extraordinarily spinous Lichadidae and Odontopleuridae, which disappeared in the Lower Carboniferous, show comparable over-specialization in a different direction; while Carboniferous and Permian Proëtidae combine the features of multiple pygidia with warty outgrowths from the carapace. *Phillipsia* (Pl. viii. fig. 4, and Pl. xii. fig. 7) and *Griffithides* are two well-known genera from the Carboniferous Limestone. Proparia disappeared in the Devonian, but were represented by three of their four families in that period. Spinous species of *Homalonotus* marked the decline of the Calymenidae, *Crotalocephala* is the end-form of the Cheiruridae; while a fairly extensive series of Phacopidae showed gerontic features in simplification of the glabella, warty ornamentation, and, in some cases, degeneration of the compound eyes.

True Malacostraca occur first in the Carboniferous, though certain problematical Isopods have been described from the Devonian. The group was but feebly represented in the Upper Palaeozoic.

Arachnids of the *Limulus*-type are not uncommon in the Coal Measures (where they are often beautifully preserved in ironstone nodules), but *Limulus* itself is not known before the Trias. *Cyclur*, *Belinurus* (Pl. xii. fig. 8) and *Prestwichia* are well-known Carboniferous types, the last bearing a remarkable general resemblance to Trilobites. Eurypterids are familiar fossils of the Old Red Sandstone, where their often enormous size and grotesque form are clearly gerontic characters, preparatory to their imminent extinction. *Pterygotus*, *Slimonia* (Pl. xii. fig. 9) and *Stylonurus* are among the most familiar British genera. The last-named type sometimes attained a length of nearly six feet. *Eurypterus* itself is rare in the Old Red Sandstone, but occurs in the Coal Measures and is known by one survivor in the Permian.

Scorpions and Spiders occur in some variety in the Coal Measures, where they are accompanied by Myriopods. That group appeared first in the Lower Old Red Sandstone of Scotland. The most prolific locality for discovery of Carboniferous Arthropods in England is at Sparth Bottoms, near Rochdale.

The Insecta, which show such overwhelming preponderance in the recent fauna, are found first in the Carboniferous. Great numbers of types occur there, but almost all belong to extinct orders. In some respects these early forms were synthetic, combining features now distributed among distinct orders. Insect-wings (often dangerously like "fern" pinnules) are not uncommon in the shales of the British Coal Measures, but the most noteworthy locality for Carboniferous Insecta is undoubtedly the district of Commentry, in France.

CHAPTER IV

MESOZOIC FAUNAS (PLS. XIII. AND XIV.)

(A) GENERAL ACCOUNT

WITH the exception of deposits formed under abysmal conditions, almost all types of sedimentary rocks occur in the British Mesozoic sequence. Desert sands, marls accumulated in inland (often acrid) water, fluviatile, deltaic and marine strata constitute the rocks at various horizons and localities. Further, the deposits of marine origin range from littoral sands and oolites through argillaceous series to true pelagic ooze. Opportunities are thus afforded for the preservation of very varied faunal assemblages, while the recurrent local variations of physiography provide more or less continuous records of several types.

Of the four periods into which the Mesozoic era is divided, the two earliest are extremely unsatisfactory (from the standpoint of Palaeontology) in their British development. Practically all parts of the Triassic system are virtually unfossiliferous; while the Rhaetic is represented by a layer rarely exceeding twenty feet in thickness. By way of compensation, the Jurassic and Cretaceous strata are not only highly fossiliferous, but have retained their organic contents in an admirable state of preservation. Fossils from the Lias, Oolites and Chalk attract attention by their intrinsic beauty, and often form no inconsiderable bulk of the heterogeneous collections of curiosities displayed in the cabinets of Victorian drawing-rooms.

The early Mesozoic history of the British area is directly continuous with that of Permian times. During an interval that may well have extended through half the era, the terrestrial, mainly desert, conditions that succeeded the Pennine uplift were maintained. Enclosed patches of water that survived through the Permian period passed through the several stages of desiccation until the whole area was covered with shifting sand-dunes and wind-swept loess. The Rhaetic stage had prevailed over Southern Europe long before any modification of Triassic conditions affected this area. Just before the close of the Rhaetic period, marine encroachment and steady, though local, isostatic depression, brought the coastal waters of the Mid-European sea over parts of "Britain," and let in a gulf from the "Atlantic" in the north-western parts of the district. The main Rhaetic coastline passed from the eastern slopes of Dartmoor northwards to the neighbourhood of Cardiff, and then took a north-easterly course, past the south of the Pennines to North Yorkshire, with a westerly extension towards the Cheshire plain. A large island or peninsula covered much of Eastern and South-Eastern England, so that the sea area was of the nature of a strait widening at its two extremities. In no part of the British area was it possible to get far from land. The inroad of the sea over the Triassic desert-surface resulted in adulteration of the water by solution of incrustations. The "Rhaetic Bone-Bed" and a curiously limited Invertebrate fauna bear testimony to the unhealthy quality of the Rhaetic coastal belt.

The chief features of Rhaetic topography were maintained through the Jurassic period—all British deposits of that stage having been formed within detrital limits. Liassic strata are largely argillaceous; shales and clays become interbedded with sands and littoral

limestones in the Oolitic series. Throughout the Jurassic period conditions comparable with those of the Coal Measures (on a small scale) obtained around the Highland coasts; and estuarine deposits form the bulk of Lower Oolitic strata in Northern England. Towards the close of the Oolitic stage delta-formation was shifted to the southern area, and the huge, but local, mass of the Purbeck-Wealden series was formed.

The Cretaceous period was marked by the commencement of gradual and continuous depression, whereby the amount of land in the area was steadily diminished. Although its main coastline seems not to have passed much farther westwards than that of the Rhaetic, the Cretaceous sea became open by submergence of the "Eastern Isle." Littoral facies of Upper Cretaceous rocks remain in such fragmentary deposits as those of Haldon Hill in Devonshire, the Hibernian Greensand of Antrim, and outliers in and near the Isle of Mull. But calcareous ooze, often almost free from detrital matter, represents the typical product of this phase. Upheaval brought these thalassic conditions to an end, but the stages of its operation are lost (in Britain) by much denudation of the Upper Chalk in pre-Eocene times.

The Mesozoic era is often called the "age of Reptiles," and no more appropriate designation could be applied. But there are many features in the Invertebrate fauna of the era that are equally as distinctive, if not so superficially evident, as the reptilian régime. In Britain there is a particularly marked contrast between the faunas of the Upper Palaeozoic and Mesozoic strata. This diversity is not entirely due to the long Permo-Triassic interval during which very scanty palaeontological records are available. In other regions, where fossiliferous Permian is overlain by equally prolific Trias, the extinction of old types and inception of

new ones is manifest. Tetracoralla, Stromatoporoids, Blastoids, Camerate Crinoids, Perischoechinoids, Cryptostome and Trepostome Polyzoa, Orthid, Strophomenid, Productid and Spiriferid Brachiopods, many groups of Pelecypods and Gastropods, Orthoceratid and Goniatitic Cephalopods, Trilobites and Eurypterids, are some of the more important series of Upper Palaeozoic Invertebrates that either failed to survive the Permian, or lingered, reduced to almost negligible proportions, into the Mesozoic. In place of the heavy casualties in Permo-Triassic evolution, appeared the Hexacorals, true Echinoids, Rhynchonellid and Terebratulid Brachiopods, Oysters and Trigonias, Naticas and Pleurotomarias, and, above all, Ammonites and Belemnites. Many of these types had been in existence in the Upper Palaeozoic, but their prominence was postponed until the Trias. In like fashion, most of the types predominant in the Cainozoic had their origin in the Trias (the Mammalia being noteworthy), but were content with a lowly position in Mesozoic faunas.

(B) PROTOZOA

Foraminifera are usually abundant, even to a rock-forming degree, in Mesozoic deposits, but Radiolaria are less conspicuous. The former group was sparingly developed in the Trias (absent from British "New Red Sandstones"), but in Jurassic clays and limestones it began to show that diversity and abundance that culminated in the Upper Cretaceous. As regards the quality of the tests, Mesozoic Foraminifera are closely comparable with those of the present day—calcareous, multiperforate types predominating over arenaceous forms. The most important series of the latter type is that of the Lituolidae; some members of the family

secrete siliceous skeletons in which agglutinated matter is subordinate. The imperforate, porcellaneous tests of Miliolidae are often found, but vitro-calcareous Textulariids, Lagenids and Globigerinids constituted the bulk of the Mesozoic Foraminiferan fauna. Most types are small, but such genera as *Cristellaria* and *Frondicularia* often attained sufficient size in the Chalk to allow of detection with the naked eye, even in the field.

Radiolaria are far from abundant in British Mesozoic deposits. From the records available in other districts, it would seem that the Nasselaria, inferior to the Spumellaria in older periods of the era, overtook and almost outnumbered the more primitive types in the Cretaceous.

(C) PORIFERA

Owing to the scarcity of deep-water deposits of Mesozoic age, the Silicispongiae of that era are usually less abundant than the Calcispongiae. Only in the Chalk (in this country) can siliceous forms be called common, but there they occur in such quantities as to be responsible, in large measure, for the production of flint. The semi-parasitic Monactinellid genus *Cliona* has left its crypts in many Cretaceous shells (Pl. iv. fig. 5); Megamorine Lithistids, such as *Doryderma*, form the nuclei of many curiously shaped flint-nodules; Tetracladine forms (e.g. *Siphonia* and *Jerea*) account for much of the Upper Greensand chert; while the exquisite tracery of Dictyonine Hexactinellids (ranging back to the Trias) is spread over much of the Chalk in beds of slow accretion. *Coscinopora* and *Ventriculites* abound (as impressions) in the "rock-bands" of the Upper Chalk, desilicified by percolating water. In many cases their remains have been phosphatized; in some they have retained the more massive parts of their siliceous

skeletons within the sanctuary of flint-nodules constructed out of the ruins of their dermal spicules (Pl. ii. fig. 2).

In parts of the Oolites, and in the Lower Cretaceous, Calcareous Sponges (especially Pharetrones) are sufficiently numerous to rank as subordinate rock-formers. In the Lower Bathonian of Dorsetshire *Holcospongia* and *Raphidonema* form well-marked "Sponge-beds"; while the Aptian "Sponge gravels" of Faringdon are famed for the abundance of many species of the latter genus. The Sycon *Barroisia* is fairly common in that deposit.

(D) COELENTERATA

The Oolitic stage is the only part of the Mesozoic sequence of Britain in which coral-reefs are found, although scattered corals (usually solitary forms) occur at all horizons from the Lias to the Chalk. Practically all Mesozoic Corals are Hexacoralla; and, in the absence of Stromatoporoids and Graptolites, they constitute most of the Coelenterate record of the era. Most known families of Hexacorals appeared in the Trias or Lias, and Mesozoic members of the group bear a strong resemblance to those still living. The great family of the *Astraeidae* is represented by *Montlivaltia* among solitary types, and by *Isastraea* (Pl. xiii. fig. 1) and *Thecosmilia* (chiefly in the Oolites) among reef-builders. Of the other families, the small *Anabaciidae* are common in the Lower Oolites, and the massive *Thamnasteria* and *Stylina* are important in the Corallian. The last (perhaps also the first) of the Tabulata, *Chaetetes*, lingered throughout the era, and may be found in some abundance in the Inferior Oolite of the Mendip area.

There are but few corals in British Cretaceous rocks; they are typified by such small, solitary forms as *Trochocyathus* and *Parasmilia*. But in the Upper

Cretaceous two presumably Hydrozoan genera appear in considerable profusion. *Parkeria* is a common fossil of the Cambridge Greensand, and *Porosphaera* is familiar (and zonally valuable) to all workers in the Upper Chalk. Both of these genera are considered to be nearly allied to *Hydractinia*, but they have been referred by some observers to the Porifera or even to the Foraminifera.

(E) ECHINODERMATA

Although some forms of Crinoidea are locally abundant, and fragments of Stelleroids occur in most marine deposits, Echinoids are the predominant Mesozoic Echinodermata. The rapidity of specialization and wealth of variety, shown by that class during the era, are in accord with its exuberant neanic elaboration in the Upper Palaeozoic. So numerous (and withal beautiful) are fossil Sea-Urchins in the Oolites and Chalk, that the utter absence of Cystids, Edrioasteroids, Blastoids, and Adunate and Camerate Crinoids is insufficient to reduce the interest and importance of the phylum.

Inadunate Monocyclic Crinoids, the sole surviving order of the subclass, are fully represented; the most noteworthy type is *Saccocoma*, best known from the Solenhofen Stone, but found in the British Kimmeridgian. This small "feather-star" was one of the very few Monocyclic types to assume "eleutherozoic" habits by atrophy of the stem; the quality was developed, and is maintained, in the majority of Dicyclic Flexibilia.

Dendrocrinoid Dicyclic Inadunata are especially abundant in Mesozoic deposits. *Encrinus*, the type of the whole class, occurs as a rock-former in the Triassic Muschelkalk. *Pentacrinus*, a side-line of the persistent *Isocrinus*-lineage, is a familiar fossil of the Lower Lias;

its pentagonal columnals abound in rocks of Jurassic age. The two most peculiar Inadunates are *Uintacrinus* and *Marsupites*, both restricted to the Upper Cretaceous. Unlike most free-swimming Crinoids, these types increased, rather than reduced, the size of their calyces, the former by incorporation of numerous small brachials (a secondary "Camerate" quality), the latter by enlargement of the plates of the normal cycles. Both types had exceedingly short careers, that of *Uintacrinus* immediately preceding that of *Marsupites*. They are used as zonal indices in the Upper Chalk. Flexibilia were equally important in the Mesozoic. *Apiocrinus* (the "pear-encrinite") (Pl. xiii. fig. 2) is a well-known Bathonian type. Specimens complete from root to crown have been found in the Bradford Clay; the discoid columnals are abundant on slabs of Forest Marble. *Bourgueticrinus*, a small allied genus, is universally abundant in the Upper Chalk; its varied shape has some zonal significance. *Rhizocrinus* continues this series in modern faunas. Free-swimming types of this order predominate at the present day, and were well differentiated in the Mesozoic. The small size and delicate construction of "Feather-Stars" make them rare and obscure in the fossil state. *Millericrinus* (Pl. i. fig. 3), a type locally abundant in the Bathonian and Corallian, though akin to *Apiocrinus*, shows an early stage in atrophy of the stem. *Antedon* (*sens. lat.*) is known from the Lias, and may often be collected during search for Chalk Microzoa.

Holothurians of essentially modern aspect occur in Solenhofen "Slate." Stelleroids are abundant throughout the era, but entire specimens are rare. *Ophioderma* produces a local "starfish-bed" in the Middle Lias. Large marginals of Phanerozonate Asteroids are abundant in the Oolites, and ubiquitous in the Chalk.

Fragmentary though they are, these ossicles illustrate clearly the satisfactory palaeontological characters of Echinoderms, in that zonal and morphological points of great importance can be ascertained from them. *Astropecten* in the Stonesfield Slate and Callovian, and *Metopaster* in the Chalk, are Phanerozonte forms sometimes found in an unbroken condition.

Euechinoidea seem to date from the Trias. It is unfortunate that Lower Mesozoic rocks in Britain are ill-suited for preserving their remains. During Triassic and Liassic times most of the orders of Echinoids were differentiated, but they could not live in deserts and shunned muddy water, so that our record of the class was practically postponed until the Oolitic stage, by which time most types were well established.

The Cidaroida are undoubtedly the simplest, and apparently the oldest, of Euechinoidea. They were developed from Archaeocidaroid forms by reduction of interambulacral columns to two, and loss of coronal imbrication. Much of this change was achieved in the Permian; and Triassic Cidaroids, apart from vestiges of flexibility, were much like those still living. This morphogenetic stagnation of the order gives yet another illustration of the persistence of primitive forms; *Lingula* and *Nucula* are the analogues of *Cidaris* in their respective phyla. *Cidaris* (*sens. lat.*) occurs in the Lower Lias and Rhaetic, but is common only in clear-water deposits of Oolitic and Cretaceous age (Pl. xiii. fig. 3). In the Inferior Oolite, Corallian and Chalk, complete or fragmentary tests and radioles are often abundant. The Diademoid (Centrechinoid) order seems to have branched from the Cidaroid in Triassic times, perhaps before full coronal rigidity had been attained. The dominant characteristics of this group are progressive ambulacral complexity and multiplication of

radioles. Both of these qualities were carried far during the Mesozoic, but have been yet more elaborated in later times. Small, somewhat obscure, forms, usually ascribed to *Acrosalenia* and *Hemipedina*, occur in the Rhaetic and Lias. The Inferior Oolite is rich in species of *Pseudodiadema*, *Hemipedina* and *Stomechinus*; *Hemicidaris* and *Acrosalenia* are important in the Bathonian. The Corallian is one of the most prolific horizons for Diademoida (coral-reefs are favourite resorts of modern types); *Hemicidaris* and *Diplopodia* are represented by abundant and characteristic species. The latter genus, with small forms of *Salenia* and *Peltastes*, predominated in the Lower Cretaceous; *Phymosoma* (Pl. xiii. fig. 4), with greater ambulacral complexity than is usual in Mesozoic forms, is sometimes common in the Chalk. The probably regressive Echinothuriidae, represented by the "collapsible" genera *Asthenosoma* and *Phormosoma* at the present day, were foreshadowed by *Pelanechinus* in the Corallian and *Echinothuria* in the Chalk.

The "Regular" orders were joined by their "Irregular" offspring in the Lias, if not before. Two distinct orders, with very different morphogenetic qualities, are certainly known from that period. Holectypoida, the least "Irregular" of their kind, are represented by *Plesiechinus*, which became abundant in the Bajocian; *Pygaster* continued this stock in the Corallian. *Holectypus*, differing from the Pygasteridae in the posterior position of the periproct, is known from the Upper Lias, and has abundant species in the Lower Oolites, Cornbrash and Corallian. *Discoidea*, an important and ambulacrally elaborate descendant of *Holectypus*, is essentially a Lower Cretaceous and Lower Chalk genus; *Conulus* ranged throughout the Chalk, but is abundant only at restricted horizons.

Nucleolitoida, which show much greater advances

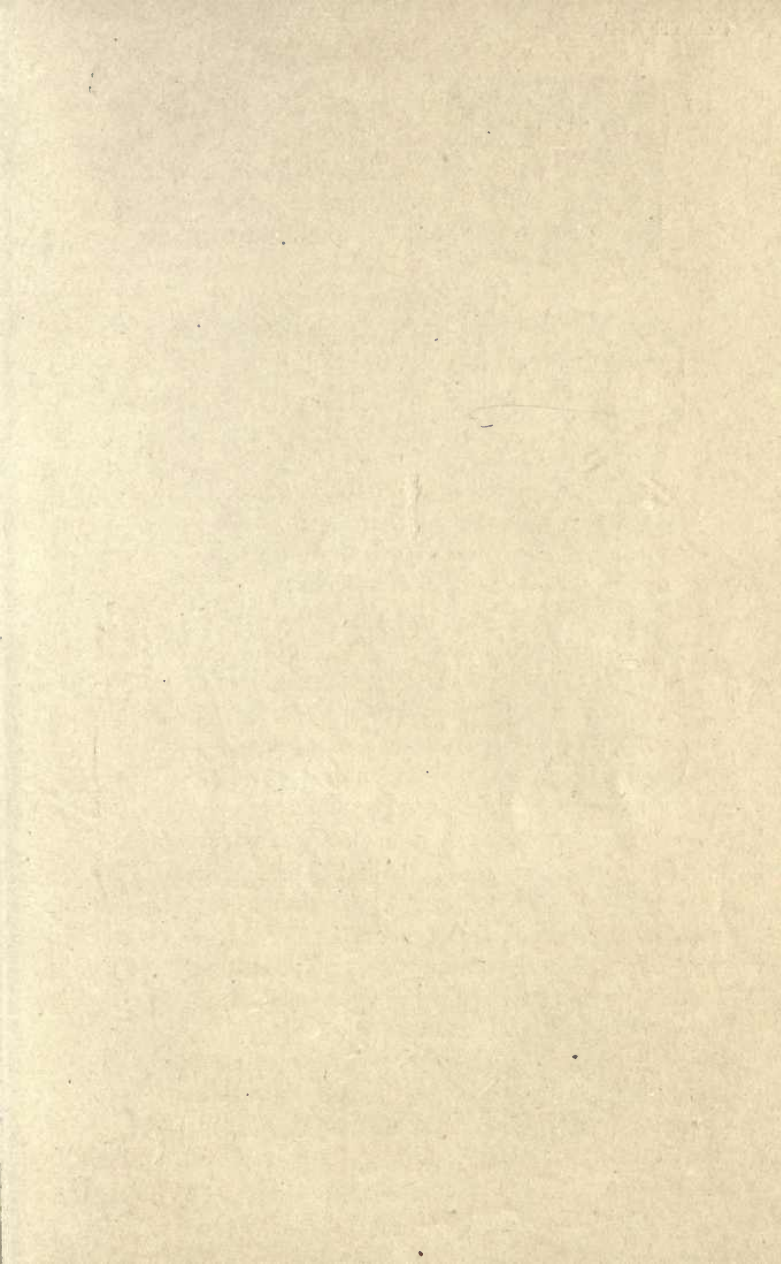
towards "Heart-Urchin" characters than even the latest Holoctypoids, were represented in the Lias by *Galero-pygus*, which, like *Plesiechinus*, is abundant in the Inferior Oolite. At that horizon it was joined by *Nucleolites*, *Clypeus* and *Pygurus*. Gigantic tests of *Clypeus sinuatus* give the name to the "*Clypeus-grit*," of Bathonian age, in the Coteswolds. The species is historically interesting, having been recorded, and credited with sundry virtues, in the seventeenth century. *Nucleolites* (Pl. xiii. fig. 5), one of the simpler genera of its order, is not uncommon in the Cornbrash, and often swarms in the Corallian. It can boast of a single surviving species. *Pygurus* lingered to the Lower Cretaceous, but is rarely common in this country. The Collyritidae, a peculiar group of small Echinoids (probably an aberrant offshoot from the Nucleolitoid stock), are represented by abundant species of *Pygorrhysis* in the Inferior Oolite. *Hyboclypus*, from the same stage, was perhaps an incompletely specialized member of the family. Spatangoida appeared at the beginning of the Cretaceous period, and at once attained great prominence. The imperfectly cordiform Echinocorythidae are particularly characteristic of the period, but persist in deep water at the present day. *Holaster* supplies two zonal indices to the Chalk, and comprises many other common Upper Cretaceous species. *Echinocorys*, an essentially Upper Chalk genus, can be found at all horizons in that stage, and gives valuable stratigraphical evidence by its protean changes of form. The small *Offaster* is characteristic of high zones. True Heart-Urchins (Spatangidae) are even more abundant. *Hemiaster* is not uncommon in the Gault and Grey Chalk, but its few British species give little indication of the overwhelming vigour of differentiation shown elsewhere by Cretaceous members of the stock. *Epiaster*

is rare in low zones of the Chalk, but abundant at higher horizons. *Micraster* (Pl. xiii. fig. 6) is especially dominant in the Upper Chalk. Two zones are "named" after species of the genus; but without any attempt at specific determination it is possible to recognize the precise horizon of any *Micraster* by its form and surface-details. The genus has supplied some of the most satisfactory material available for tracing the evolution of continuous series living amid uniform surroundings.

(F) POLYZOA

Apart from a few representatives of the Ctenostomata, Mesozoic Polyzoa were either Cyclostomata or Cheilostomata. The former order showed a marked re-awakening of specialization as compared with its Upper Palaeozoic dormancy. The Cerioporina perpetuated many of the characters of the Ceramoporoidea (from which they may have been derived), and encrusting forms, such as *Berenicea* and *Idmonea*, spread abundantly over the shells and rock-surfaces of the era. It is quite exceptional to collect specimens of Chalk Irregular Echinoids that are free from colonies of those forms. The Cheilostomata (which are probably direct descendants of the Cryptostomata) first appeared in the Jurassic, but did not become abundant until the Upper Cretaceous. Sheets of *Membranipora* are commonly found associated with encrusting Cyclostomata on Chalk fossils, and free-growing types are constant, though fragmentary, ingredients of "flint meal."

Perhaps the most important Polyzoan fauna in the British Mesozoic is that of the Faringdon "Sponge-Gravels" of Aptian age. In most parts of this local facies of "Greensand" the Sponges are subordinate to Cyclostomatous Polyzoa in quantity and variety. The



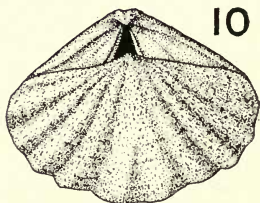
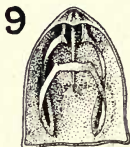
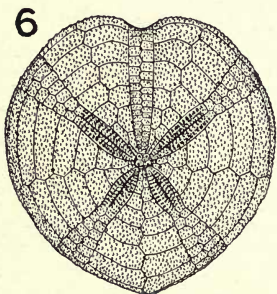
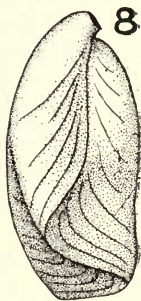
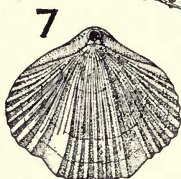
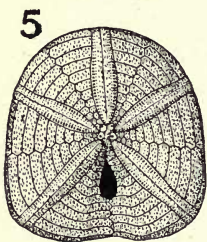
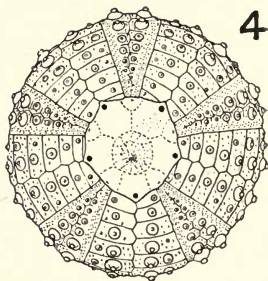
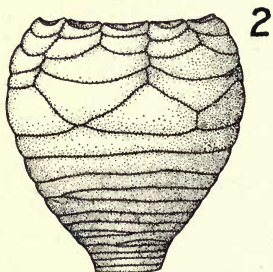
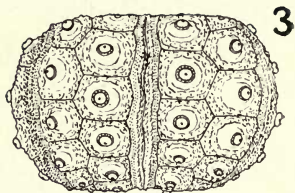
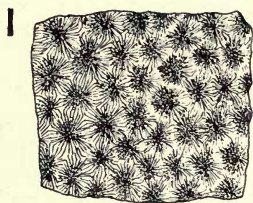
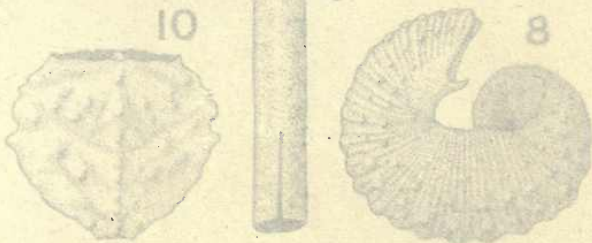




PLATE XIII

MESOZOIC FOSSILS

- FIG. 1. *Isastraea explanata*. Corallian, Shellingford, Berks.
- FIG. 2. *Apiocrinus parkinsoni*. Bradford Clay, Bradford, Wilts.
- FIG. 3. *Paracidaris florigemma*. Corallian, Stanford in the Vale.
- FIG. 4. *Phymosoma koenigi*. Upper Chalk, near Kingsclere, Hants.
(The reconstruction of the apical system is hypothetical.)
- FIG. 5. *Nucleolites scutatus*. Corallian, Marcham, Berks.
- FIG. 6. *Micraster coranguinum*. Upper Chalk, Ecchinswell, Hants.
- FIG. 7. *Cyclothyris plicatilis*. Upper Chalk, near Newbury.
- FIG. 8. "*Terebratula*" *phillipsi*. Bathonian, Burton Bradstock, Dorset.
- FIG. 9. *Zeilleria digona*. Bradford Clay. Interior of dorsal valve.
(After Davidson.)
- FIG. 10. *Spiriferina* cf. *walcotti*. Lower Lias, Timsbury, Radstock.



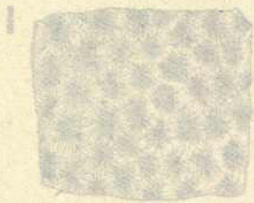


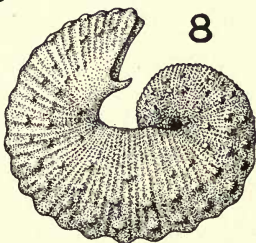
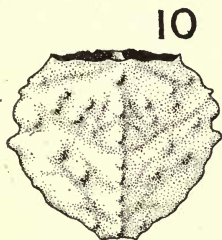
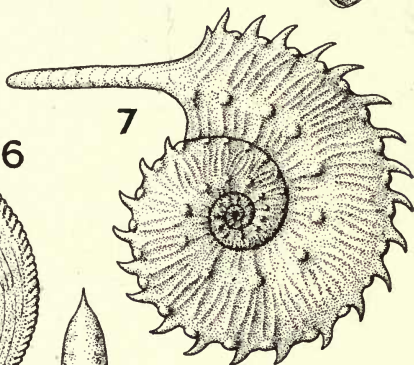
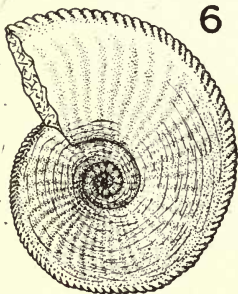
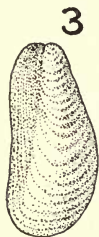
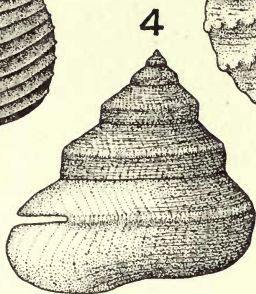
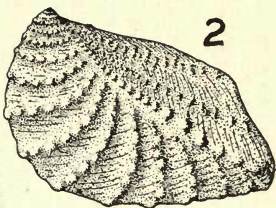
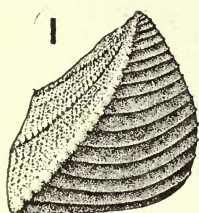
PLATE XIII

PLATE XIV

MESOZOIC FOSSILS

- FIG. 1. *Trigonia striata*. Bathonian, Burton Bradstock, Dorset.
- FIG. 2. *Trigonia clavellata*. Corallian, Marcham.
- FIG. 3. *Modiolus* sp. Bathonian, Burton Bradstock.
- FIG. 4. *Pleurotomaria reticulata*. Kimmeridge Clay, Weymouth.
- FIG. 5. "*Natica*" *bajociensis*. Bathonian, Burton Bradstock.
- FIG. 6. *Amaltheus margaritatus*. Middle Lias, Runswick Bay, Yorks.
- FIG. 7. *Cosmoceras jason*. Oxford Clay, St. Ives.
- FIG. 8. *Scaphites* sp. Upper Chalk.
- FIG. 9. *Belemnitella mucronata*. Upper Chalk, Arréton, Isle of Wight.
- FIG. 10. *Palaeocorystes* sp. Gault, Folkestone.





deposit was at one time considered to be an outlying portion of the Pliocene "Coralline Crag" on account of its Polyzoan wealth; but detailed study of the fauna showed that it marks comparable conditions of sedimentation in Lower Cretaceous times.

(G) BRACHIOPODA

Save for a few degenerate or over-specialized survivors of Atremata, Neotremata, Protremata and Spiriferacea, the Mesozoic Brachiopod fauna may be summarized by the broad "generic" terms *Rhynchonella*, *Terebratula* and *Terebratella*. *Lingula*, *Orbiculoidea* and *Crania* represented the two first orders with no greater distinction than during the Upper Palaeozoic. Small, usually cemented forms allied to *Thecidea* were the only Protremata of the Mesozoic, as they are of the present day.

The Rhynchonellids are abundant throughout the Mesozoic, and may be found at almost all marine horizons of the Liassic, Lower Oolitic and Cretaceous strata of Britain. Most of the later Mesozoic types had a sharp parapet around the pedicle-aperture, and are thence styled *Cyclothyris* (Pl. xiii. fig. 7), but a vast series of generic terms are applied to Jurassic forms. There seems a fairly steady tendency towards increasing delicacy of ornament as the group is traced from lower to higher stages. Some Lower Oolitic types, such as *Rhynchonella cynocephala*, are almost *Pugnax*-like in form and boldness of plication; while the Cretaceous facies shown in *Cyclothyris latissima* or *C. plicatilis* (Pl. xiii. fig. 7) is flattened and finely ribbed. One series, illustrated by *Acanthothyris*, developed a spinose surface suggestive of racial decadence; the genus named is locally abundant in the Inferior Oolite.

Terebratulids were almost more prominent than

Rhynchonellids in Mesozoic times. *Epithyris*, *Glossothyris* and *Musculus* showed the typical smooth surface with undulate margin (Pl. xiii. fig. 8), while *Dictyothyris* in the Great Oolite, and *Terebratulina* in the Cretaceous, exhibited features of surface-ornament unusual in the group. Many Chalk forms (e.g. "*Terebratula*" *carnea*) showed degeneration of the pedicle without any trace of accessory means of adhesion. The Terebratellids, which are the predominant group of recent Brachiopods, appeared in the Lias with the small *Megathyris*-series that still survives; while *Coenothyris*, which retained many Terebratulid features, is known from the Trias. Smooth, elongate types (e.g. *Aulacothyris*, *Microthyris* and *Zeilleria* (Pl. xiii. fig. 9)) are not uncommon in the Lower Oolites; and small, short, often superficially ornate genera (*Kingena*, *Trigonosemus*, *Magas* and *Terebratella*) are more characteristic of the Cretaceous.

The Spiriferacea were represented by two families which ranged through the Trias into the Lias, and there suffered extinction. The relatively simple and persistent Suessiidae have a familiar Liassic member in *Spiriferina* (Pl. xiii. fig. 10); Triassic relatives of this beautiful form were often cemented. The late group Athyridae similarly survived, attaining remarkable complexity (of a gerontic type) in the Alpine Trias. The double spiralia of such types as *Diplospirella* or *Koninckina* give striking testimony to the capacities of over-specialization.

(H) MOLLUSCA

The disappearance or decline of the most prolific stocks of Brachiopods at the close of the Palaeozoic era left the Mollusca in a predominant position among shell-bearing animals. But the abundance of Mesozoic Molluscs is not merely comparative—it is absolute.

Among Pelecypoda the Prionodesmacea maintained, and even increased, their profusion, while many types of Anomalodesmacea and Teleodesmacea came into prominence. Although Aspidobranchiate Gastropods showed a decline, it was by no means precipitous, and rapid differentiation of Ctenobranchiate forms more than compensated for the reduction. But it is in the overwhelming outburst of specialization in the Cephalopoda that the Molluscan wealth of the Mesozoic mainly resides. The Nautiloids were reduced to few types; but the Ammonoids reached their acme in the Trias, retaining numerical and differential preponderance throughout the Jurassic; and Belemnoids, though monotonous in form, must have swarmed in most Mesozoic seas.

Palaeoconch Pelecypoda were feebly represented in the Mesozoic by one family only (Solenopsidae) which is still living. Taxodonts are locally abundant. *Leda* and *Nucula* are not uncommon in the Lias, and the latter genus, accompanied by its near ally *Acila*, is represented by abundant and characteristic species in the Gault. *Cucullaea* is often found in the Lower Oolites and Upper Greensand, and early forms of Limopsidae and Arcidae occur in the Jurassic and Cretaceous. Schizodonts were developed to an extraordinary degree. The most important families were the Pernidae, Pteriidae, Ostreidae, Unionidae and Trigoniidae. *Gervillia*, a soleniform member of the first family, is common in shallow water deposits from the Trias to the Lower Cretaceous; *Perna* (*Pedalion*) is known from the Inferior Oolite, but is specially characteristic of the Lower Greensand; while *Inoceramus* and its allies, commencing in the Lias, are perhaps the most abundant and universal fossils of the Cretaceous period. Truly gigantic species occur in the Upper Chalk; prismatic fragments can be found in almost every quarry at any

zone in that stage. Among Pteriidae, *Pseudomonotis* is almost a rock-former in the Rhaetic, while *Pteria*, abundant in that period, is common in the Lias and Lower Oolites. Oysters belonging to all genera recognized in that protean group occurred, and abounded, throughout the era. *Ostrea* itself is a rock-former in the Lower and Middle Lias, Great Oolite, Kimmeridge Clay and Purbeck beds. *Gryphaea* is one of the best known fossils of the Lower Lias, and is common in the Oxfordian. *Alectryonia* is especially characteristic of the Oolites, but occurs abundantly in the Cretaceous; while *Exogyra* is almost restricted to the Upper Oolites and Lower Cretaceous. In the Lower Greensand, specimens of *Exogyra sinuata* more than a foot in length are not uncommon. *Cardinia*, a very common fossil of the Lower Jurassic, was possibly a descendant of the *Carbonicola*-stock of Carboniferous date. In estuarine facies of the Lower Oolites, and again in the deltaic marls of the Wealden, *Unio*, hardly to be distinguished from the fresh-water Mussels of existing rivers, occurred in some abundance. Lastly, *Trigonia* (see Pl. iii. figs. 1 and 2), sprung from *Schizodus* of the Permian (through the Triassic *Myophoria*), can be collected in hundreds at many Jurassic horizons, and maintained its abundance in the Lower Cretaceous. On the whole, there is a tendency for Lower Jurassic *Trigonia*s to have linear ornament (e.g. *T. striata*, Pl. xiv. fig. 1), while those from the Upper Oolites have pustular surfaces (e.g. *T. clavellata*, Pl. xiv. fig. 2). Morphogenetic phases showing derivation of the latter from the former type can be studied on well-preserved shells from high horizons. Three families of Isodonta were particularly prominent in the Mesozoic. Pectinidae abound in the Middle Lias and in most clear-water deposits of later date. In the Upper Cretaceous the subgenera

Aequipecten and *Chlamys* were especially important. Spondylidae, probably derived from the Pectinidae, and showing phylogerontic tendencies towards sessility, were represented by *Plicatula* and *Spondylus*, both genera being very common in the Cretaceous. Limidae are very uniformly distributed through the periods. *Plagiostoma* is common in the Lower Lias and again in the Chalk. *Limatula* and *Ctenostreon* are essentially Oolitic. The Dysodont genera *Mytilus* and *Modiolus* (Pl. xiv. fig. 3), both still living, were represented throughout the Mesozoic, the latter being especially abundant in the Rhaetic and Lower Jurassic. *Hippopodium*, a well-known Liassic type, is probably akin to the "Mussels," and seems continuous with the Silurian *Modiolopsis*-series.

The small order Anomalodesmacea was more fully developed in Mesozoic than later periods. *Pleuromya* and *Gresslya* were two abundant genera of the Pleuromyacidae, a family restricted to the era. The former genus is especially common in the Inferior Oolite and Portlandian. *Pholadomya* and *Goniomya* similarly represented another family, but the former has one species still living. It is especially abundant in the Lower Lias and Inferior Oolite.

Among Teleodesmacea, all types of hinge-structure appeared, although the most abundant Mesozoic forms had the relatively simple "Diogenodont" dentition. *Trapezium* and *Arctica* (*Cyprina*) represented the Cypricardiacea; *Astarte*, *Crassinella* and *Opis* are common Astartacea of the Oolites (the first-named being more important in the Cainozoic); while *Cyrena* (abundant in the Wealden), *Cardita* and *Diceras* (especially Neocomian) introduced their respective super-families. The most extraordinary series of Pelecypoda known, the Rudistacea, were probably derived from the last-named type. They were massive, sessile forms re-

sembling operculate Corals more than other Mollusca; their morphogenetic analogues are to be found in the Richthofeniid Brachiopods of the Permian. Like them, *Radiolites* and *Hippurites* were phylogerontic forms of short duration. They were absolutely restricted to the Cretaceous period, and played the part of rock-formers in some districts. Though rare in the English Chalk, they are not uncommon in littoral deposits such as the Cambridge Greensand. Lucinacea were represented by *Tancredia* (especially Jurassic), *Lucina* and *Sphaera* (Lower Cretaceous). Among Cyclodonts the Cardiidae ("Cockles") were well developed, but they are rarely common. *Protocardia* is locally abundant in the Portlandian and Blackdown Greensand. Teleodonts are rare in the Mesozoic, but representatives of most families appeared in or before the Cretaceous period; while *Corbula* and many burrowing forms illustrated the degenerate Asthenodonta.

Scaphopods are rarely important fossils, but *Laevidentalium* is locally abundant in the Lias, and *Antalis* in the Gault.

Mesozoic Gastropods are chiefly remarkable for the decline of Aspidobranchs, and the rise of Ctenobranchs and Tectibranchs. *Pleurotomaria* (Pl. xiv. fig. 4) carried on the Palaeozoic tradition, and maintained its importance throughout the era; while Trochonematidae (e.g. *Amberleya* and *Cirrus*) are abundant in the Jurassic, and Trochidae, Neritopsidae and Neritidae occur locally. Gymnoglossa are represented by *Bourgetia* in the Corallian; Ptenoglossa by *Scalaria* (*Epitonium*) and *Solarium*, both abundant in the Cretaceous. Many important types of Taenioglossa appeared. Massive species of *Purpuroidea* are common in the Great Oolite, and *Littorina*, *Capulus* and *Natica* (Pl. xiv. fig. 5) occur in the Bajocian and Bathonian. The last series is

abundant also in the Gault (*Gyrodes*). The fresh-water *Vivipara* (*Paludina*) is a local rock-former in the Wealden. *Turritella*, *Cerithium* and *Aporrhais* are especially Cainozoic forms, but they had some abundant species in the Mesozoic, the first and last being particularly common in the Selbornian. A peculiar series, the Nerineidae, with complex internal folds, is characteristic of the era, *Nerinea* being especially abundant in the Great Oolite and Corallian. *Rachiglossa* and *Toxoglossa*, which attain remarkable differentiation in modern faunas, appeared first in the Cretaceous, but are rarely found in British strata of that age.

The small group of Tectibranchiate Euthyneura reached its maximum in the Mesozoic. *Actaeonina*, *Cylindrites* and *Tornatellaea* are common Jurassic fossils. Pulmonata are represented but sparingly.

Nautiloid Cephalopods were restricted to *Nautilus* and genera with similar form. *Nautilus* itself is an essentially Mesozoic genus (often attaining great profusion), and is the sole modern survivor of its order. Ammonoids reached a dazzling acme in the Trias, but geological conditions make them inaccessible to British collectors at that period. Nevertheless, from the Lias to the Cretaceous they are the most abundant and striking fossils of most horizons. The greatest degree of septal complexity was attained by *Pinacoceras* in the Trias, while small forms akin to *Lobites* reached the fullest stage of involution in the same period. But phylogerontic forms, such as *Cochloceras* and *Rhabdoceras*, mark the failure of some lineages at the opening of Mesozoic time. The most abundant Ammonites of the Lower Lias are *Tragophylloceras* (Phylloceratidae), *Psiloceras*, *Coroniceras* and *Asteroceras* (Aegoceratidae), and *Oxynticeras* (? Amaltheidae). Common Middle Lias genera are chiefly Amaltheidae (*Amaltheus*, Pl. xiv. fig. 6).

In the Upper Lias *Phylloceras* represented its family, *Hildoceras* was an early Harpoceratid, and *Dactylioceras* (Pl. iv. fig. 3), *Peronoceras* (Pl. iv. fig. 4) and *Cocloceras* introduced the important Stephanoceratidae.

Lower Oolitic genera were, in the main, members of the last two families. *Lioceras* (Pl. v. fig. 1), *Ludwigia*, *Oppelia* and *Strigoceras* are abundant Bajocian and Bathonian Harpoceratidae, and *Stephanoceras*, *Sphaeroceras*, *Morphoceras* and *Parkinsonia* (Pl. viii. fig. 1) gave similar representation to the Stephanoceratid stock. *Macrocephalites* was a genus of that family, especially characteristic of the Cornbrash and Callovian. *Lytoceras* was a long-lived type whose presumed Cretaceous descendants showed many points of interest. Ammonites show a marked decrease in abundance in the Upper Jurassic. *Cardioceras* and *Perisphinctes* continued the *Stephanoceras* tradition in Oxfordian and higher horizons respectively; while the Cosmocerotidae (a mainly Cretaceous family) were introduced by *Cosmoceras* (Pl. xiv. fig. 7) in the Oxford Clay. *Aspidoceras* was a form restricted to the Upper Oolites; it often occurs as loosely-fitting coils of internal moulds of the chambers, giving a "vertebrate" appearance that justifies the application of the term "snake-stones" to Ammonites.

In the Lower Cretaceous, gerontic acceleration, coupled with lapse of many previously important types, became abundantly manifest. *Olcostephanus* was one of the latest of the Stephanoceratidae, *Hoplites* represented the Cosmocerotidae, and *Desmoceras* introduced a new family with thickened or constricted apertures. *Ancyloceras* (a Cosmocerotid) showed "uncoiling" characteristic of late evolutionary stages. Upper Cretaceous Ammonoids were the last of their kind. Forms associated with the Lytoceratidae showed the influence of phylogerontic specialization in shell-form. *Hamites*

(common in the Gault) prepared the way for *Baculites* (chiefly Chalk Marl and Chalk Rock in Britain), in which the straight shell is superficially like that of *Bactrites*, though retaining elaborate sutures. *Turrilites*, common in the Lower Chalk, showed deceptive resemblance to a Gastropod. Cosmoceratidae were represented by *Hoplites* (common in the Gault), *Acanthoceras* (Cenomanian) and unrolled forms such as *Crioceras*, *Ancyloceras* and *Scaphites* (Pl. xiv. fig. 8). The last genus is sometimes abundant in the Lower Chalk and Chalk Rock. *Pachydiscus*, at the last-named horizon, brought the Desmoceratidae to a close; while *Schloenbachia*, one of the commonest fossils of the Chalk Marl, represented a family (Prionotropidae) whose members were strangely reminiscent of the Triassic Ceratitidae. At this stage forms with intense involution, but septal simplification, appeared. *Indoceras*, and especially *Tissotia*, had sutures almost identical with those of *Ceratites*. No Ammonites survived the Upper Cretaceous. In the British Chalk their remains are rare except in the lowest zones and the shallow-water facies represented by "rock-bands."

Dibranchiate Cephalopoda made their first appearance in the Trias (*Aulacoceras*), and the Belemnitidae vie with the Ammonoids in abundance throughout British marine Mesozoic strata. In the Lias especially their guards are so thickly congested as to constitute local rock-formers. Very large species occur in the Oxfordian, small ones are more characteristic of the Upper Oolites and Lower Cretaceous. The well-known *Belemnitella* (Pl. xiv. fig. 9) was one of the latest British members of the family; it is used as a zonal index in the higher parts of the Chalk. Degenerate forms with reduced guards persisted into the Eocene, but the Belemnitidae were essentially a Mesozoic family. The allied Belemnoteuthidae had a similar, but more re-

stricted, range. Specimens showing the chitinous hooks of the tentacles, and the "ink-bag" with its contents, are not uncommon in the Lias and Oxford Clay. Occasional representatives of the Sepioidea (Cuttle-fish) have been found in the Lias and later strata. The first of the Octopoda (*Calais*) occurs in the Upper Cretaceous of Lebanon.

(K) ARTHROPODA

The Triassic period, though poor in Arthropod remains, must have been a critical time in the evolution of the phylum. Practically all the orders characteristic of the Palaeozoic failed to survive the Permian, and those of the Lias had a markedly modern aspect. Mesozoic Crustacea were mostly Ostracoda, Cirripedia and Malacostraca. The first-named group is excessively abundant in many parts of the British Wealden, and occurs in profusion in the Chalk, sometimes outnumbering even the Foraminifera. Barnacles of such familiar recent types as *Pollicipes* and *Scalpellum* were well represented in Jurassic, and particularly Cretaceous, deposits. Isopods (Wood-lice) are usually rare fossils, but *Archaeoniscus* occurs in local swarms in the Purbeck beds, especially in the Vale of Wardour. True Decapods (Crabs and Lobsters) appeared first in the Trias. The lithographic stone of Solenhofen (Upper Oolitic) contains beautifully preserved specimens of *Eryon*; the prawn-like *Glyphaea* and crab *Palaeocorystes* (Pl. xiv. fig. 10) are not uncommon in the Stonesfield Slate and Selbornian respectively.

Arachnids, Myriopods and Insects are not well known from British Mesozoic strata, although "beetle-cases" are common in the Lias and Stonesfield Slate. Those insects that occur seem referable to existing orders, showing in this character a marked contrast from Palaeozoic types.

CHAPTER V

CAINOZOIC FAUNAS (PLS. XV. AND XVI.)

(A) GENERAL ACCOUNT

FOSSILIFEROUS Tertiary deposits in Britain are not only small in bulk and restricted in distribution, but show considerable monotony in formation and composition. Marine strata constitute a relatively small proportion, and always show signs of shallow, almost littoral, origin. Permanent presence of an important area of land since Cretaceous times ensured a plentiful supply of detrital matter; since the two main areas of Lower Tertiary sedimentation (the London and Hampshire Basins) corresponded with the estuaries of drainage-systems, sand, but especially clay, are the chief deposits. Such limestones as occur are either marine shell-beaches or fresh-water lake-marl. Typical Pliocene strata, though less argillaceous than those of the Eocene, were even more definitely coastal in formation.

Hence the British record of Cainozoic faunas is far from representative. Within its limited range it is often extraordinarily full. Mollusca in particular occur in immense numbers. But as a qualifying factor there has to be recorded the existence of such deposits as the Reading Clays and Bagshot Sands, which are almost absolutely unfossiliferous. The absence of any definite Miocene strata, and the largely lacustrine origin of much of the Oligocene, further interfere with the continuity of the faunal record.

Following the upheaval that brought Chalk formation to an end, a long interval of denudation supervened. At length the South-Eastern parts of the British area became depressed sufficiently for accumulation of lasting sediment. At the outset of this episode estuarine sands and clays seem to have spread, with practical continuity, from Suffolk to the Isle of Wight; but this broad area shortly became divided into two troughs separated by the Wealden axis of upheaval. In the London Basin increased, but localized, "sagging" admitted the sea during formation of the London Clay; but a reverse tendency followed, whereby sedimentation (save for fluvatile deposits) was prevented. In the Hampshire Basin a similar series of events occurred, but they were extended over a longer period of time, and produced a greater bulk of sediment. Not until the Upper Eocene (when the London Basin was "full") did the sea gain undisputed sway in the southern trough. The succeeding Oligocene strata mark a renewal of the struggle between land and sea, comprising deposits that are estuarine or lacustrine in the main. With the infilling of the Hampshire Basin, sedimentation (of a durable type) ceased in Britain; the whole area may have undergone considerable elevation during the Miocene period. In Pliocene times the "North Sea" covered parts of East Anglia that are now land, and left thin, but characteristic, layers of "crag" and clay. These are overlain by deposits suggestive of conditions like those prevalent in the Wash at the present day. The fossils of the sub-glacial peats and marls give clear and convincing evidence of the approaching climatic rigours of the Lower Pleistocene; but apart from their boreal aspect they are essentially modern in facies. Pleistocene deposits are largely Boulder Clay and similar glacial relics; the fluvatile and peaty beds

that occur among them contain few Invertebrate remains.

The Cainozoic era is the "age of Mammals and Birds." After long stagnation in the Mesozoic, the warm-blooded descendants of Permian Theromorphs and Triassic Dinosaurs have, by deferred neanic acceleration, amply and worthily assumed the sovereignty abdicated by senescent Reptiles in the Cretaceous period. But in the humbler sphere of Invertebrate life a comparable revolution can be recorded. The teeming Rhynchonellas and Terebratulas of the Mesozoic are reduced to insignificant numbers; Trigonias and many other Prionodesmacean Bivalves suffer a like fate; Pleurotomarias sink almost to extinction; Ammonites have entirely gone, and Belemnites are represented by scarce, usually small, descendants that bear little superficial resemblance to their predecessors. Many of the dominant Cainozoic types appeared in previous epochs (like the Mammalia), but postponed active specialization until the Eocene. Most of the Teleodesmacean Pelecypoda, Ctenobranchiate and Pulmonate Gastropoda, and Nummulitid and Globigerinid Foraminifera belong to this class. "Cake-Urchins" and "Sand-Dollars" (Clypeastroids) are exclusively Cainozoic, while burrowing "Heart-Urchins" (Spatangids), though locally abundant in the Cretaceous, are essentially Tertiary forms.

It is appropriate in this place to lay emphasis on the fact that there is no contrast between existing faunas and those of preceding Cainozoic periods that can compare with that distinguishing Eocene from Cretaceous groups. There is no Palaeontological warrant for recognition of a "Quaternary" era. Indeed, it may be doubted if Cainozoic history has yet reached its middle phase.

(B) PROTOZOA

The outstanding features in the Foraminiferan fauna of the Cainozoic era are the remarkable abundance, size and elaboration of Nummulitids and Miliolids in the earlier periods, and the overwhelming predominance of Globigerinids in later and existing times. The coin-like tests of *Nummulites* often attained diameters exceeding two inches; they were the chief limestone-builders in the Mediterranean district during the Eocene and Oligocene. Miliolids play a corresponding part in the construction of the well-known Eocene "Calcaire grossier." Vast numbers of small Nummulitids (*Nummulina*) and relatively large Miliolids (*Alveolina*) occur in some of the Upper Eocene clays of the Isle of Wight, but Foraminifera are never rock-formers in British Tertiary strata. *Globigerina* is the most abundant constituent of foraminiferal ooze in the late Tertiary and Holocene.

Radiolaria are well represented in many districts, and their remains, practically unaltered, are sometimes sufficiently abundant to have an economic value. The well-known "Barbados Earth," and the equally famous "Tripoli Powder," are nothing more than deposits of uncompacted Radiolarian ooze. They are used as polishing powder and for dilution of explosives. Both these deposits are of Miocene age, but the majority of genera composing them are still living. Nassellaria are considerably in excess of Spumellaria, and their grotesque, but exquisite, tests are familiar to all microscopists.

(C) PORIFERA

Remains of Sponges are rare in British Tertiary deposits. The muddy and often estuarine conditions prevalent in sedimentation areas were uncongenial to

Poriferan life. Silicispongiae are very feebly represented in the Cainozoic, but their rarity as fossils must be ascribed to the infrequent occurrence of deposits formed in the deep water where these types abound at the present day. The case of the Calcispongiae is different. The Pharetrones, which were of chief importance in the Jurassic and Lower Cretaceous, are unknown from the Tertiary, and seem to have suffered the fate normal to vigorous groups. The Sycones still linger, but in diminished numbers. The horny sponges (which are unknown in the fossil state) are the most conspicuous members of the phylum in modern faunas.

(D) COELENTERATA

Tertiary Coelenterata are very feebly represented in Britain. Save for a few stunted Madreporaria (such as *Turbinolia*) and occasional composite types (e.g. *Litharaea*), they are hardly to be found in the Lower Tertiaries; while *Flabellum* (Pl. xv. fig. 1) and *Balanophyllia* are the only important genera that lived in the cooling climate of the Pliocene. *Hydractinia* sometimes encrusts shells found in the Crag. On the whole, the Tertiary Coelenterate fauna proves, as far as it goes, to be closely akin to that still extant.

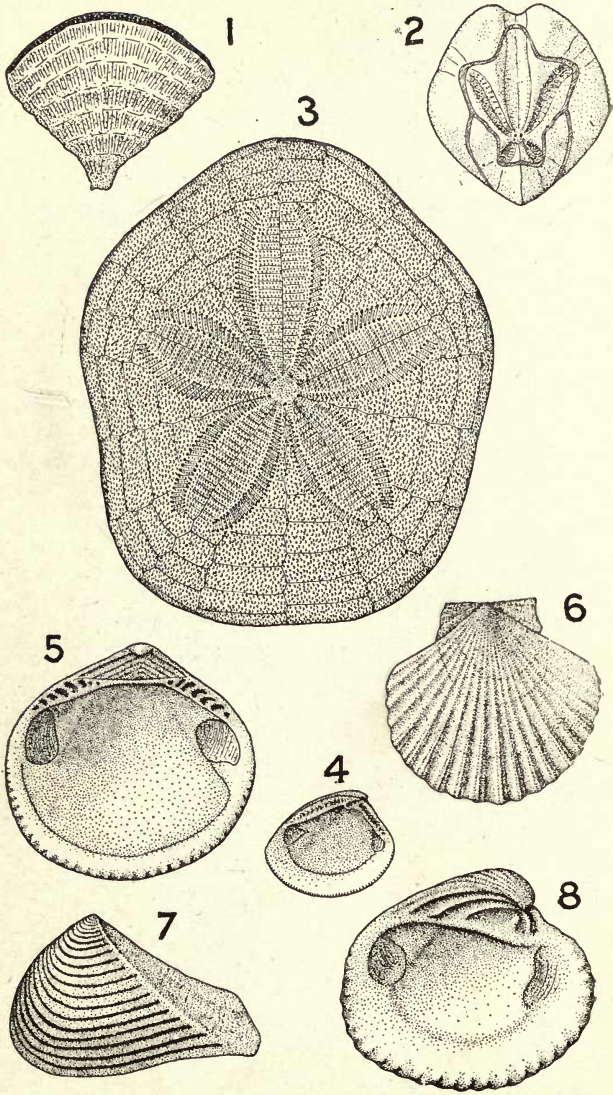
(E) ECHINODERMATA

The preference shown by Echinoderms for clean surroundings, and their distaste for brackish water, cause the British record of Tertiary forms to be lamentably meagre. Save for a few (probably drifted) fragments of Crinoids in the London Clay, associated with occasional Ophiurids and burrowing Spatangids, and an insignificant series of practically modern forms in the Crag, no evidence of the remarkable abundance and

variety developed by Feather-Stars, Starfish, Brittle-Stars and Sea-Urchins is available in this country until the present period is reached. In some measure this scarcity of fossils in the Tertiary may be ascribed to the reduction in massively-built types of Echinoderms begun in Mesozoic times. Stalked Crinoids are rare, and have usually retreated to abysmal depths. Their eleutherozoic offspring are too delicate for normal preservation. Modern Stelleroids are overwhelmingly numerous, but most of them seem even less suited for fossilization than their ancestors. The abundance of Echinoids, which are eminently adapted for preservation (whether massive rock-dwellers or flimsy burrowers) in Cainozoic rocks of other districts no less than in modern faunas, shifts the responsibility for the feebleness of the British record on to physiographical conditions.

Crinoid remains are always rare in the Tertiary. *Isocrinus* (usually represented by columnals) occurs in the London Clay, and the genus is the least rare of living stalked types. Such Stelleroids as are known are essentially modern in facies.

Both Regular and Irregular Echinoids seem near to their acmes in the modern fauna, and their tests occur in rock-forming profusion in the Mediterranean region and parts of North America. The Cidaroida show little change, in structure or numbers, but they seem to have betaken themselves to parts of the sea remote from littoral belts (on which they flourished in Jurassic times). The Saleniid series of Diademoida is comparably retiring, and has dwindled to very small faunal proportions. The Arbacioid series (with ambulacral structure similar to that of *Hemicidaris*) is fully represented by *Arbacia* and *Coelopleurus*, the latter being abundant in Indian Miocene deposits. *Diadema* (*Centrechinus*) is apparently a reversionary member of its



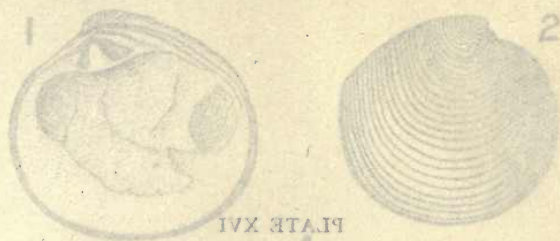
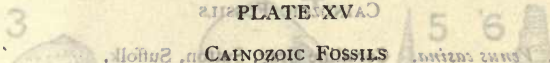


PLATE XVII



- FIG. 1. *Flabellum woodi*. Red Crag, Walton-on-the-Naze.
 FIG. 2. *Schizaster scillae*. Miocene. (Tubercular ornament omitted.)
 FIG. 3. *Clypeaster altus*. Miocene. (Plan of adapical surface.)
 FIG. 4. *Nucula headonensis*. Oligocene, Isle of Wight.
 FIG. 5. *Glycimeris glycimeris*. Red Crag, Suffolk.
 FIG. 6. *Aequipecten opercularis*. Coralline Crag, Sutton, Suffolk.
 FIG. 7. *Crassatellites sulcatus*. Eocene, Barton, Hants.
 FIG. 8. *Venericardia* ("Cardita") *planicosta*. Eocene (Bracklesham beds); Whitecliff Bay, Isle of Wight.



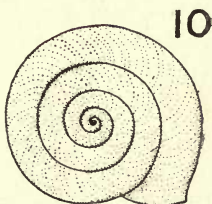
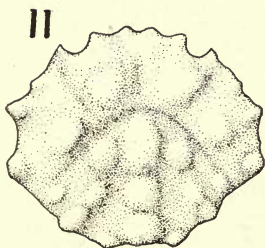
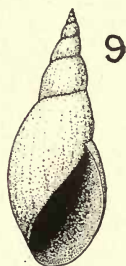
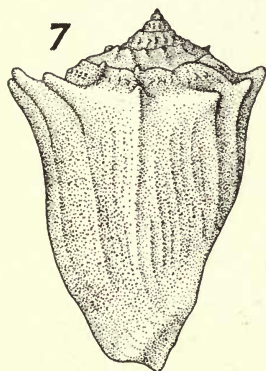
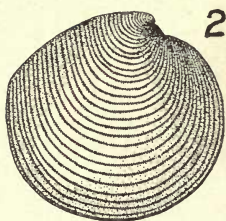
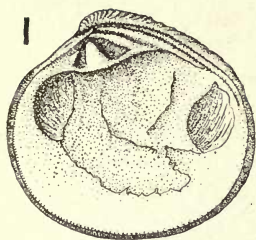


PLATE XVI

CAINOZOIC FOSSILS

- FIG. 1. *Venus casina*. Coralline Crag, Sutton, Suffolk.
- FIG. 2. *Dosinia exoleta*. Red Crag, Walton-on-the-Naze.
- FIG. 3. *Nerita aperta*. Oligocene, Headon Hill, Isle of Wight.
- FIG. 4. *Ampullina patula*. Eocene, Barton, Hants.
- FIG. 5. *Turritella imbricata*. Eocene (Bracklesham beds), Whitecliff Bay, Isle of Wight.
- FIG. 6. *Batillaria serrata*. Eocene (Calcaire grossier).
- FIG. 7. *Volutilithes athletus*. Eocene, Barton, Hants.
- FIG. 8. *Surcula* ("Pleurotoma") *teretrium*. Eocene, Barton, Hants.
- FIG. 9. *Limnaea longiscata*. Oligocene, Headon Hill, Isle of Wight.
- FIG. 10. *Planorbis euomphalus*. Oligocene, Bembridge, Isle of Wight.
- FIG. 11. *Xanthopsis bispinosa*. Eocene, Sheppey.





group. *Echinus*, and a number of allied genera, have, on the contrary, reached a sufficient acme at present. *E. esculentus* abounds around rocky districts of modern shores, and a closely similar species occurs, usually in a much shattered condition, in the East Anglian Pliocene. The predominant Cainozoic group of Regular Echinoids is the Echinometridae. *Parasalenia*, which arose in the Eocene, is not much advanced beyond the *Echinus*-stage of elaboration, but *Strongylocentrotus* (which is locally abundant on British rocky fore-shores), *Echinometra* and *Heterocentrotus* (tropical genera) show the highest degree of specialization known in the subclass.

Among Irregular Echinoids, the Holoctypoida have dwindled to the solitary genus *Echinonëus*, which is found fossil in the Mediterranean region, but lives on the other side of the Atlantic at present. However, direct descendants of the Holoctypoid Discoidiidae, the Clypeastroida, have shown an extraordinary evolutionary activity throughout the era. Small, retarded forms, such as *Echinocyamus*, occur in the British Pliocene and live around our shores to-day, but the main stream of Clypeastroid progress has flowed in subtropical climates. In the Eocene, Miocene and Oligocene rocks of the Mediterranean area, small discoid forms like *Sismondia* and *Scutellina* are overshadowed by the extreme variety and numbers of large Clypeastridae and Scutellidae. *Clypeaster* (Pl. xv. fig. 3), *Scutella* and *Encope* are perhaps the chief genera, and from the Himalayas to the Andes are local rock-formers at every Cainozoic stage. Nucleolitoids are only not extinct, but their place is taken by the true Cassiduloida, which, in such genera as *Echinolampas*, vie with the Clypeastroids for supremacy. Heart-Urchins are hardly less abundant, but the delicacy of their tests makes them less con-

spicuous than the massive surface-dwellers. *Schizaster* (which occurs in local clusters in the London Clay) competes with the Cretaceous *Hemiaster* in specific differentiation (Pl. xv. fig. 2), while *Brissus*, *Brissopsis*, *Echinocardium*, *Moiria* and *Spatangus* help to prove the continuity of Cainozoic with recent faunas.

(F) POLYZOA

The most noteworthy assemblage of Polyzoa in British Tertiary strata is that of the Coralline Crag of the East Anglian Pliocene. Cyclostomata are there represented by massive colonies of *Theonaa*, *Alveolaria* and *Hornera*, but they are inferior in numbers to the Cheilostomata, of which *Retepora* is the most familiar genus. This proportion of the two important orders of Gymnolaemata is that normal to Tertiary faunas. Apart from the Crag, Polyzoa are rare in the argillaceous or sandy deposits of the British Tertiary, but at the present day *Membranipora* and *Flustra* abound in shallow water around the coasts.

(G) BRACHIOPODA

The only series of Brachiopoda to show any phyletic vigour in Cainozoic times is that of the Terebratulacea, and among them the Terebratellids (the latest group to arise) alone attain faunal prominence. It may be confidently assumed that the abundance of recent genera recognized in this section is the outcome of more complete morphological knowledge, and will sink into relative insignificance as continued study is applied to fossil types.

The Lingulids, Thecidiidae and Craniidae continue their unassuming progress throughout the era, and the Rhynchonellids are hardly more important. *Terebratula*

is represented in the British Eocene, and again by such large species as *T. perforata* in the East Anglian Pliocene; but throughout the Cainozoic the Terebratelloids seem to have favoured the clear and austral waters that they now inhabit. Of Cainozoic Brachiopoda it must be confessed that rarity makes them stratigraphically negligible, and similarity to recent types reduces their palaeontological interest. Reflecting upon the overwhelming importance of the phylum in Palaeozoic times, and the abundance of some groups in the Mesozoic, it is impossible to repress the sentiment contained in the hackneyed quotation *Sic transit gloria*.

(H) MOLLUSCA

Tertiary Mollusca have a definitely modern facies. Not only are the proportionate values of the several orders maintained without change from the Eocene to the present day, but a great number of genera have persisted throughout the era. Reduction and degeneracy in the Cephalopoda are more than counter-balanced by extreme diversity in Pelecypoda and Gastropoda. The extraordinary abundance of terrestrial forms of the latter order in modern faunas is probably deceptive—their choice of habitat denies them ordinary chances of fossilization. But Teleodesmacean Bivalves and Ctenobranchiate Univalves show a real increase (foreshadowed in the Cretaceous period), and their usual preference for muddy coastal water has enabled them to leave abundant remains in British Cainozoic deposits.

Although Teleodesmacea are the predominant Pelecypoda of to-day, the old-established Prionodesmacea are still important, and may even oust their more progressive relatives locally. Taxodonts are represented

by *Nucula* (which is often common in the Lower Tertiaries of the Hampshire Basin, Pl. xv. fig. 4), *Cucullaea* (chiefly in the Woolwich beds) and *Glycimeris* (Pl. iii. fig. 4 and Pl. xv. fig. 5). The last genus, so abundant on recent beaches, is found in the Eocene, but is especially characteristic of the Pliocene. Among Schizodonts, great reduction on Mesozoic numbers has to be noted. *Pinna* is one of the few surviving types of the Pteriacea; it is not uncommon in the London Clay. The *Inoceramus*-series has disappeared, but *Perna* still lingers, and even *Gervillia* has been found in the Eocene. The Ostreidae are the only Schizodont family to maintain supremacy, and *Ostrea* itself (Pl. iii. fig. 5), common in all brackish-water facies of the Tertiary, shows few signs of decline at the present day. *Unio* occurs in some profusion in Oligocene clays; but *Trigonia* is always scarce in the Cainozoic, and is represented by few living species. The Isodonts retain some measure of their Mesozoic importance. *Pecten* (Pl. xv. fig. 6), *Spondylus* and *Anomia* are the predominant types. The first is especially abundant in the Pliocene. Many recent species of *Spondylus* show complete fixation in Oyster-fashion—apparently indicative of phylogerontic specialization akin to that prevalent in many Brachiopod lineages. *Modiolus* and *Mytilus* represent the Dysodonts, but the latter is less abundant in the fossil state than its modern exuberance would suggest.

Anomalodesmacea are distinctly less prominent than in the Mesozoic. *Pholadomya* still persists, and is common in the London Clay. *Thracia*, a genus that made its appearance in the Trias, is best known in Britain from the Pliocene.

Teleodesmacea are developed in overwhelming numbers. The Diogenodonts, which were the only

members of the order to attain importance in the Mesozoic, are fully represented in the Tertiary. Large species of *Arctica* are common in the London Clay and Coralline Crag. *Astarte* is especially abundant in the Pliocene, *Crassatellites* (Pl. xv. fig. 7) in the Eocene. *Corbicula* is common in fresh-water Oligocene deposits, and *Cardita* (Pl. xv. fig. 8) abounds in the Bracklesham and Barton series. *Chama* (especially at the latter horizon) represents the persistent radical from which the Cretaceous Rudistae sprang. *Lucina* and *Corbis* are common throughout the era. Cyclodonts are abundantly illustrated by the Cardiidae, *Protocardia* and *Discors* are especially frequent in the Eocene, *Cardium* itself is common in the Crag. Teleodonts are the predominant forms. *Venus* (Pl. xvi. fig. 1), *Dosinia* (Pl. xvi. fig. 2), *Meretrix* and *Paphia* have numerous species in the later Cainozoic; *Tellina*, *Macoma*, *Psammobia* and *Donax* are no less common as fossils than on modern beaches. Though far from rare in the Eocene, they are particularly common in the Pliocene. *Macra* and *Spisula* are no less abundant. Asthenodonts are more fully specialized and differentiated in the Cainozoic than before. The well-known genus *Mya* is important in the Pliocene, *Corbula* abounds in the Oligocene, *Panope* is common in the London Clay, and *Teredo* (the ship-worm) riddled drift-wood in the Eocene estuary of the London Basin.

In spite of the abundance of Bivalves, Gastropods are undoubtedly the dominant Molluscan class of the Cainozoic. Aspidobranchs make up in numbers what they lack in variety; Ctenobranchs show both qualities; while Pulmonates carry univalve supremacy on to unfamiliar ground. The venerable *Patella* (a "*Lingula*" among Gastropods) seems incorrigibly successful. The small "slit-limpets" (e.g. *Emarginula*) are common

Pliocene fossils; but *Pleurotomaria* can show only four living species (and few post-Cretaceous ones) of great rarity. The small Trochidae and Neritidae are the most successful series of recent Aspidobranchs. *Trochus* is abundant in the Pliocene; *Nerita* (Pl. xvi. fig. 3) and *Neritina* swarm in the Oligocene, their shells often retaining traces of coloration. Among Ctenobranchiata, Gymnoglossa are represented by small forms akin to *Turbonilla*, but they are never common. *Scalaria* is an abundant genus of Ptenoglossa. Taenioglossa are very fully developed. *Littorina*, which congregates in swarms on modern coasts, is hardly less abundant in the Pliocene. *Capulus* emulates *Patella* in persistence as in form; *Calyptraea* and *Xenophora* are essentially Cainozoic genera. Naticidae with greatly inflated body-whorls (*Ampullina*, Pl. xvi. fig. 4) are among the commonest fossils of the Eocene, and abound in the Crag. Fresh-water Viviparidae, strikingly like *Vivipara* of modern rivers, are common in the Oligocene. *Turritella* (Pl. xvi. fig. 5) is at its best in the Eocene, some species attaining very great size. *Melania*, *Cerithium* (Pl. xvi. fig. 6) and *Potamides* are common throughout the Tertiary, the two first occurring in marine deposits, the last in brackish layers of the Oligocene. *Aporrhais* is a well-known Pliocene fossil; while the small *Rimella* and gigantic *Hippochrenes* abound in the Eocene. Cowries are especially Cainozoic forms; *Trivia* occurs profusely in the Pliocene and Pleistocene. Large species of *Pyrula* are common in the London Clay.

Rachiglossa and Toxoglossa are pre-eminently Tertiary groups. The former are represented by abundant Buccinidae ("whelks") throughout the era, *Buccinum*, *Pisania*, *Nassa*, *Strepsidura*, *Melongena* and *Neptunea* being the most important genera. The last-named is particularly interesting, in that its most

characteristic Pliocene species was sinistral, while modern types are normally dextral. Spinous Muricidae are hardly less abundant; *Typhis*, with small shells ornamented by hollow excrescences, being especially common in the Barton Clay. *Purpura* (*Thais*) is abundant in the Pliocene, as at present. The Fusidae are one of the most familiar Cainozoic families. *Fusus* is common in the Eocene, and is there associated with gerontic side-lines such as *Sycum* and *Clavella*. The Barton Clay is particularly famed for its abundant Volutidae; scores of exquisite forms of *Volutilithes* (Pl. xvi. fig. 7) occur, together with the less ornate species of *Lyria*. *Maculopeplum* is a well-known Pliocene genus. The chief families of Toxoglossa are the Turritidae and Conidae. *Turris* (*Pleurotoma*, Pl. xvi. fig. 8), divided into numerous sub-genera, is common throughout the Eocene; *Conus*, while enjoying its acme at the present day, is well represented by less involute forms (*Conorbis*) in the Eocene.

Curiously enrolled types, such as *Bullaria* and *Seraphs*, are familiar Tertiary members of the Tectibranch Euthyneura, but it is in the Pulmonate section that the subclass finds its fullest Cainozoic expression. *Limnaea* (Pl. xvi. fig. 9) and *Planorbis* (Pl. xvi. fig. 10), represented by species closely resembling modern types, are largely responsible for the Bembridge Limestone, and occur abundantly in other fresh-water Oligocene strata, especially the Headon Beds. Snails are usually scarce as fossils, but *Helix* (*sens. lat.*) and *Amphidromus* are not uncommon in the Bembridge Beds. The degenerate shells of Slugs are occasionally found in the same deposit.

Cainozoic Cephalopoda call for little palaeontological comment. Nautiloids are almost restricted to the family Nautilidae, one species of *Nautilus* still surviving. Large

species of that genus, accompanied by the end-forms of the Clydonautilidae (*Aturia*), occur in the London Clay. Ammonoids are altogether wanting, but degenerate Belemnoids (e.g. *Beloptera*), with insignificant guards, lingered into the Eocene. The recent *Spirula*, with a coiled, almost "Gyroceracone," shell, seems to show development of long-deferred enrolment in this usually "Orthoceracone" group. Cuttle-fish and Octopods occur sparingly. The majority of the latter are devoid of hard-parts, and their frequently gigantic proportions suggest phylogerontic over-development comparable with that of the Elephants.

(K) ARTHROPODA

Little comment is needed on Cainozoic Arthropods. The prevalent orders are those dominant at the present day; a large proportion of genera have persisted from the Eocene. The common "acorn-barnacle" (*Balanus*) first appeared in the Eocene; it is abundant in the Pliocene Crags. Crabs and Lobsters are common in the London Clay, especially in the Isle of Sheppey. *Hoploparia* and *Xanthopsis* (Pl. xvi. fig. 11) are well-known representatives of the two series. More delicate Arthropoda, such as Myriopoda and Insecta, are best known by forms enclosed in amber (usually of Oligocene date); but an abundant and wonderfully preserved insect-fauna has been discovered in fresh-water marls at Florissant, Colorado. Lepidoptera, Diptera and Hymenoptera of essentially modern aspect, often retaining much of their coloration, have been found in that remarkable deposit. Specimens enclosed in amber are normally perfect and uncompressed. Knowledge of small forms such as the Diptera is made accessible by such a mode of preservation.

CHAPTER VI

CRISES IN EVOLUTION

SUBDIVISION of the foregoing outline of faunal progress into sections, although strictly orthodox and almost inevitable, cannot fail to lay undue emphasis on the apparent discontinuity of evolution. It has been mentioned above that the classification of Stratigraphy was devised, and to some degree elaborated, by workers whose belief in the separate creation of successive faunas was complete. The practical utility of that scheme in these latter days, when the basis for its original adoption sounds almost ludicrous, must awaken questions as to the quality of evolutionary progress. It has been argued, in the last chapter of Part I., that the rate of evolution varies in different phases of the phylogeny of a single stock. Is it reasonable to suppose that evolution of the world-fauna is comparably susceptible to acceleration and retardation? Are there periods during which all but the most sluggish groups are unusually plastic and vigorous in differentiation? Or is the progress of Evolution uniform?

Approximately definite answers to these questions are, as yet, impossible. Until proportionate amounts of material have been collected from every horizon, and from all accessible parts of the world, no such sweeping generalizations could be other than speculative. The purpose of the following sentences (which are primarily addressed to residents in the British Isles) is to

emphasize the danger of forming opinions on such a matter from the evidence provided within a small area.

In Britain, the arbitrary divisions between the Lower and Upper Palaeozoic (Proterozoic and Deuterozoic), Palaeozoic and Mesozoic, and Mesozoic and Cainozoic, conform so closely to observed facts in Stratigraphy and Palaeontology that they appear to coincide with natural breaks. Not only were the Upper Silurian, Permo-Carboniferous and Late Cretaceous periods marked by serious earth-movement (involving important physiographical changes), but they were followed by episodes which, whether in sedimentation or denudation, have left great lacunae in palaeontological evidence. In consequence, the faunas separated by these gaps in the record prove to be exceedingly different in character. The fossils of the Magnesian Limestone seem to have little connexion with those of the Rhaetic and Lias (the next truly marine series accessible in this country). Between the organisms of the Chalk sea and those of the Eocene estuaries there is a contrast that cannot wholly be ascribed to diverse physiographical conditions. It is difficult to avoid the conception that some great acceleration must have influenced evolution during the barren intervals. Where positive and negative evidence is involved, a kind of mental halation tends to magnify the impression of the former at the expense of the latter.

Indication of the unsoundness of such reasoning can be found, in purely palaeontological features, even in this country. The scanty and ill-preserved fauna of the Devonian contains a blend of types (particularly among Coelenterates, Brachiopods and Trilobites) which have as much in common with their Silurian predecessors as with their Carboniferous descendants. On stratigraphical grounds, the vast accumulation of Permo-

Triassic "New Red Sandstone," and the proofs of enormous denudation prior to the commencement of Tertiary sedimentation, must be accepted as representing long intervals of time, during which organic evolution will have made great progress, even if proceeding at its normal rate.

When the records of these critical times are studied in distant regions, the boundaries between eras often prove no less obscure than those between their several periods, both in Stratigraphy and Palaeontology. The familiar term "Permo-Trias" expresses the uncertainty surrounding separation of the Palaeozoic and Mesozoic, while the difficulty of determination of the upper limits of the Carboniferous and diversity of opinion as to the value of the Rhaetic show that the division between the two eras cannot be shifted in either direction with better hopes of precision. The Ammonites, which appear so suddenly in our Liassic record, were the descendants of forms that flourished elsewhere in Permian as well as in Triassic times. The first Belemnite certainly seems to have been Triassic, but so was the last *Orthoceras*.

In many parts of Europe there is comparable reason for hesitation in drawing a line between the Cretaceous and Eocene. The faunas of the Maëstrichtian and Danian stages (unrepresented in Britain) show steadily increasing "Tertiary" qualities as they are traced upwards. Most Cainozoic Invertebrate groups range back to the Cretaceous, if not farther; while Belemnites, at least, lingered after Mesozoic times. Teleodonts and Ctenobranchs had climbed far towards their acmes before Ammonoids disappeared.

In fine, the world-evidence at present available seems to point towards a negative answer to the two first questions asked in the opening paragraph of this chapter. It is perhaps perilously hypothetical, but at

least in accord with present knowledge, to suggest that the course of evolution can be likened to a flowing tide. One wave after another rears its crest and falls in ruin—each one rushes up the beach, only to slip back, and yield place to another which may sweep farther or fall short. Amid the welter of advance and retreat—the roar of the oncoming breaker and the hiss of its shattered recoil—it is hard to see that any lasting progress is achieved. But behind the seeming futility of each foredoomed effort, steadily and invincibly the tide is coming in.

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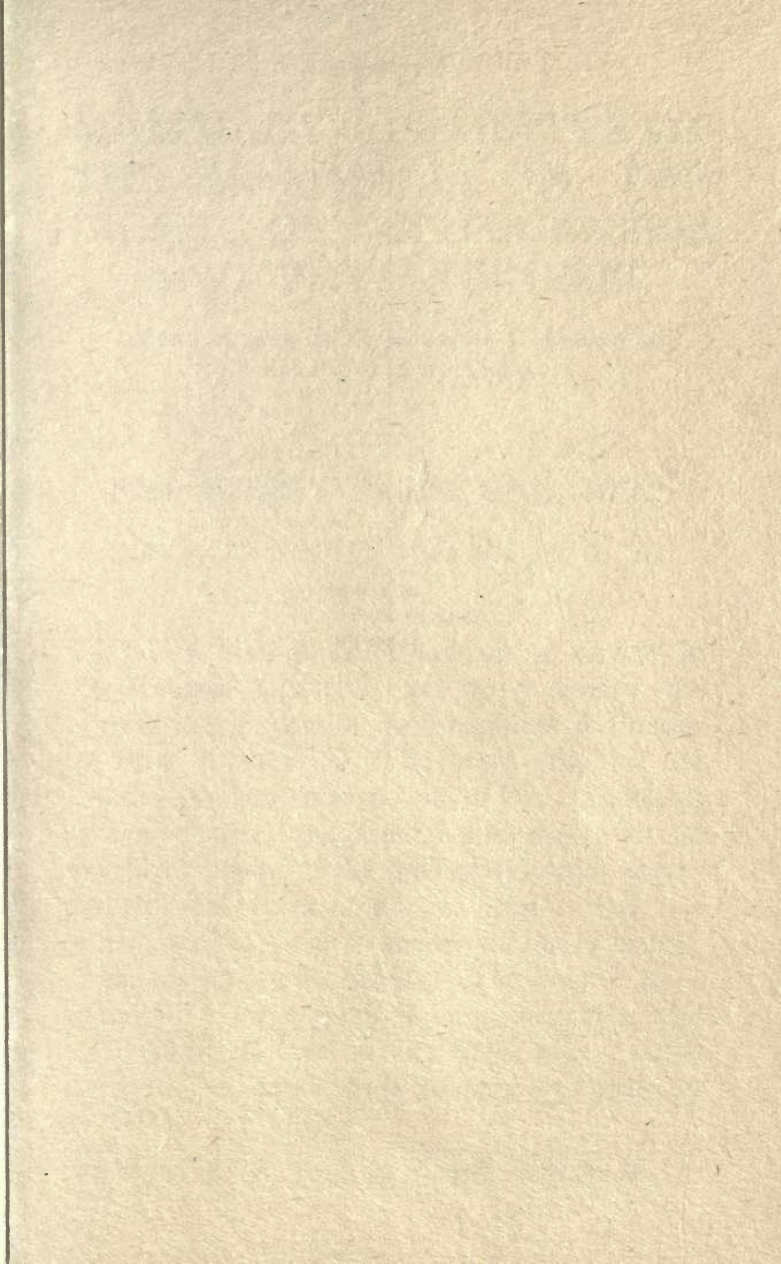
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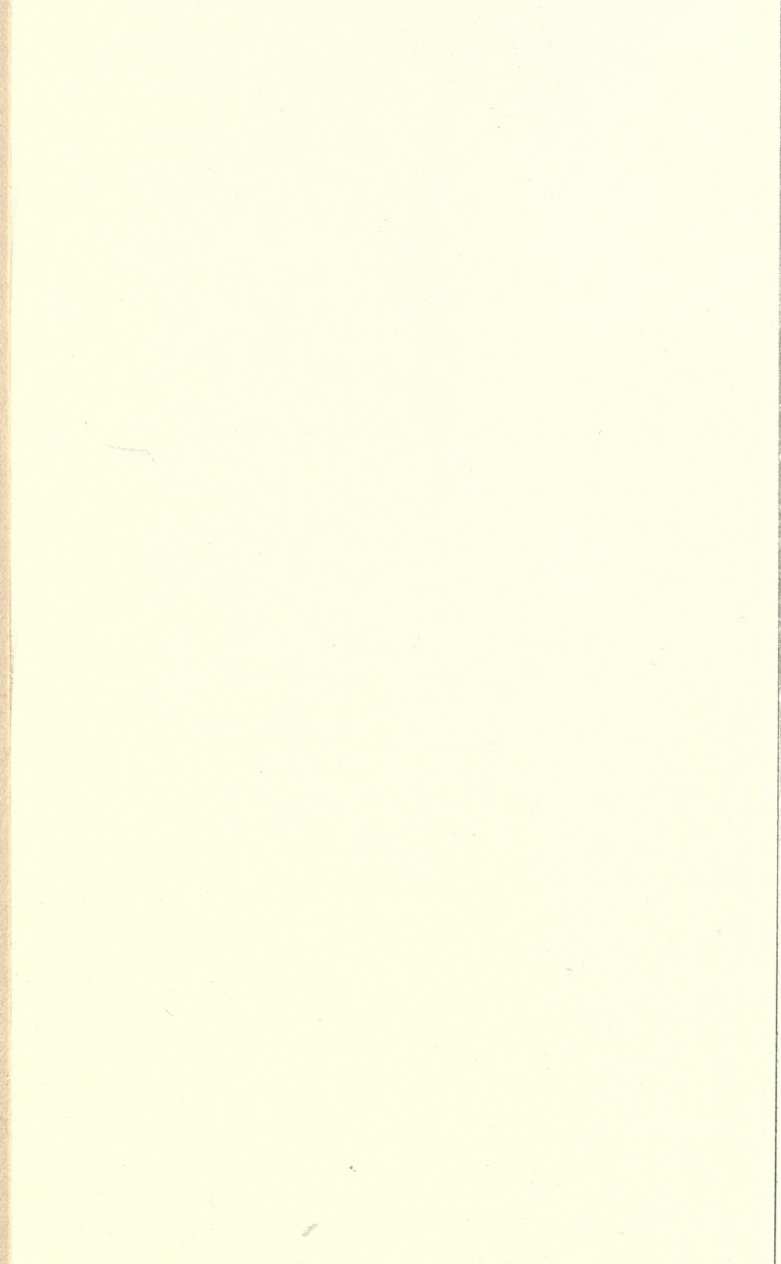
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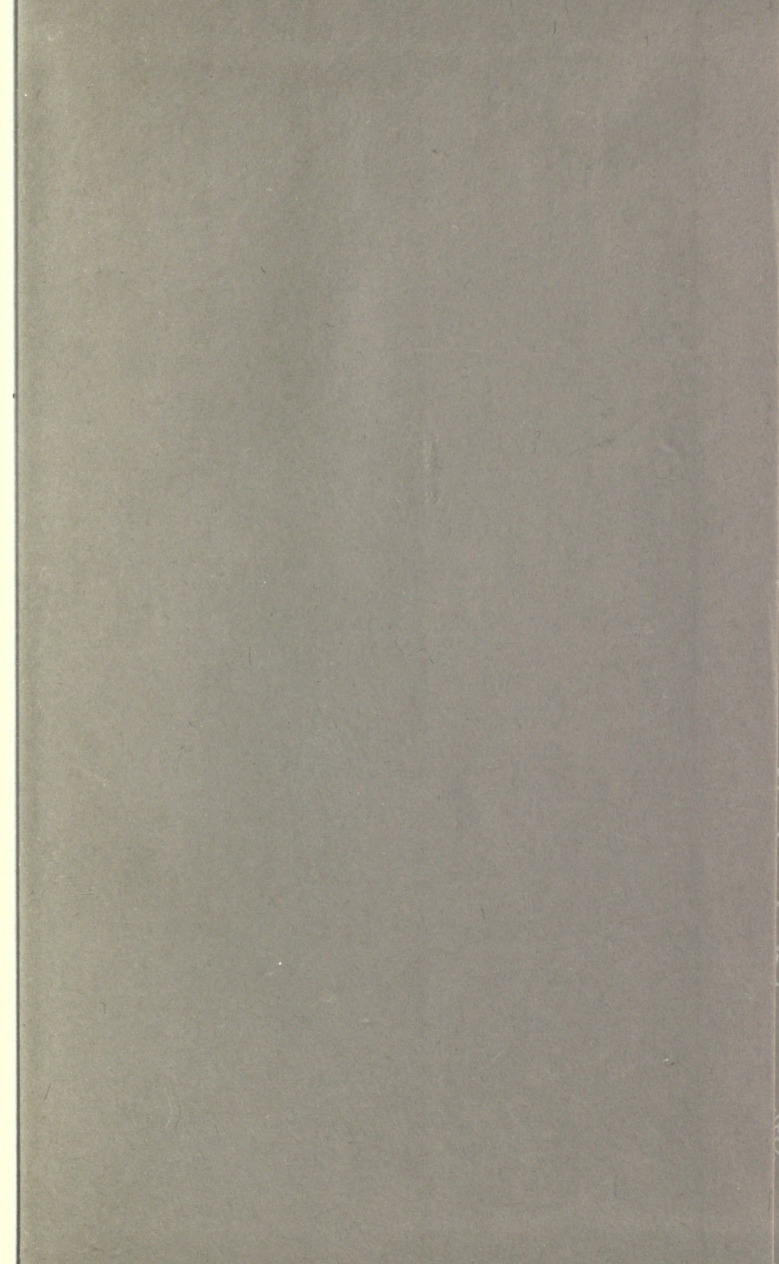
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